

**Habitat use of the bottlenose dolphins  
(*Tursiops truncatus*) of Fiordland:  
Where, why and the implications for management**

**Stephanie M. Bennington**

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**Poncho showing off in the beautiful Bowen channel of Dusky Sound**

photo credit: Steph Bennington

## Abstract

Understanding the distribution of a species gives important clues about its ecology, and can provide key information and guidance for conservation management. The bottlenose dolphins (*Tursiops truncatus*) of Fiordland, New Zealand, form three small subpopulations, two of which are mostly resident within separate fjord systems: Doubtful Sound and Dusky Sound. Within these fjords, the dolphins' distribution and resulting habitat use varies, with high and low use areas, and seasonal variation evident. In this thesis I investigated the distribution patterns of the dolphins, to better understand what drives them and how this relates to the way the dolphins are managed. Specifically, I used Kernel Density Estimation (KDE) from sighting information collected between 2005 and 2018 in Doubtful Sound, and 2009 and 2018 in Dusky Sound, to identify patterns in habitat use over time. Drivers of habitat use were investigated using species distribution models (SDMs), in the form of generalised additive models. Abiotic predictor variables were modelled using long term occurrence data as the response variable. Biotic predictors were included in SDMs for 2018, a year in which I collected data on potential prey and dolphin distribution concurrently. Information on dolphin prey was collected using Baited Underwater Video (BUV). I found that although seasonal variation in habitat use was present, general distribution patterns were consistent through time. I was able to identify some useful abiotic predictors, but found that they were generally poor at explaining dolphin distribution (Doubtful Sound top model deviance explained = 9.45%; Dusky Sound top model deviance explained = 5.20%). In Doubtful Sound during 2018, including biotic predictors improved model performance (abiotic-only model deviance explained = 19.8%; biotic predictors included deviance explained = 39.1%) and suggested that the main driver of distribution for the dolphins was the abundance of potential prey. These results are significant because they indicate the importance of particular areas within the fjords for the dolphins, and show that they remain important through time. This confirms that both populations would be good candidates for spatial based management. The results of this thesis also suggest that prey distribution plays an important role in the distribution of the dolphins and management should therefore have a more ecosystem-based focus, protecting the fish species that are important for the dolphins.

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# Chapter 1

## General Introduction

Loss of biodiversity is occurring at increasing rates on a global scale, driven in large part by the loss and degradation of habitat (Duffy 2003; Wilson et al. 2008; Pereira et al. 2010). As human populations continue to increase, our activities encroach further into wildlife habitat. Habitat loss can be obvious, such as converting old growth forests to agriculture or pine plantations (e.g. Tilman et al. 2001), or subtle, leaving it in a degraded state through direct and indirect impacts (e.g. Dudgeon et al. 2006). Indirect effects can occur in a myriad of ways, including modification of habitats (Pike et al. 2010; Wen et al. 2010), increased levels of toxins (de Kock et al. 1994; Dudgeon et al. 2006; Stockin et al. 2007), and noise pollution (Haren 2007; Ware et al. 2015).

Predators have a high extinction risk from habitat loss because they are less abundant than their prey, breed more slowly, and may have more specialised habitat use (Pimm et al. 1998; Duffy 2003). In some situations, predators exert a top-down control on the ecosystem through controlling the abundance of their prey (Estes 1994). Therefore, when removed from the system, trophic cascades and secondary extinctions may follow (Paine 1966; Estes and Palmisano 1974; Borrvall and Ebenman 2006; Krauss et al. 2010). The disproportionate effect that predators can have on the ecosystem means they are often termed keystone species (Paine 1969; Mills et al. 1993; Harley 2011). Protecting the habitat of keystone species should be a conservation priority, as this will have overarching effects for the entire ecosystem.

Among mammals, odontocete cetaceans are among the longest lived and have the lowest reproductive rates (Duncan et al. 2007). Also, their habitats are not immune to the growing trends of habitat loss and degradation worldwide. Modification of coastlines and increased pollution (e.g. by runoff from land), are directly impacting many coastal species (Crain et al. 2009). Extensive boat traffic creates high levels of noise pollution (Hooker et al. 1999; Aguilar Soto et al. 2006; Haren 2007), risk of vessel strike (van der Hoop et al. 2015), and behavioural modifications to the animals (Lusseau 2003a, b, 2006; Stockin et al. 2008a; Guerra et al. 2014). Furthermore, fisheries practises deplete prey stocks, damage benthic habitats and create flow-on effects to the wider ecosystem (Lewin et al. 2006; Wilson et al. 2010). Understanding where the core habitat is, and why these areas are important can aid in reducing human impacts through spatial management actions.

Spatial management aims to reduce human impacts within defined areas. In marine systems these are often termed Marine Protected Areas (MPAs), which include no-take marine reserves, where removing plants and animals, and modifying habitat is prohibited. Marine reserves are extremely valuable conservation tools, particularly for protecting habitat and commercially targeted fish species (Russ and Alcala 2004; Aburto-Oropeza et al. 2011). For large, mobile, marine predators, however, the area protected by marine reserves is often too small to be effective (e.g. Afonso et al. 2009). Therefore, for animals like cetaceans, MPAs that are less restrictive than marine reserves, and can be established over larger areas, are often employed. These MPAs can restrict certain activities, such as tourism (Lusseau and Higham 2004), or fishing practises known to cause marine mammal bycatch (e.g. Slooten and Dawson 2010). Understanding the distribution of the target species is essential in ensuring that MPAs effectively reduce harmful anthropogenic activities (Hooker et al. 1999).

For highly mobile species, like cetaceans, initiating effective spatial management has additional challenges, as their distributions are rarely static in time (Southall et al. 2006; Certain et al. 2007). In fact, many animals respond to changes in the environment by shifts in their distribution and resulting habitat use (Hartel et al. 2015). These shifts can drastically reduce the protection offered by spatially based management (e.g. Wilson et al. 2004; Hartel et al. 2015). A potential solution is adaptive management, whereby the effectiveness of protection is monitored, and management actions are adjusted accordingly (Cañadas et al. 2005).

### **1.1 Distribution analysis**

Distribution analyses can be used to help understand a species' ecology, and can provide key information for conservation management. A species' distribution is the result of complex interactions with the environment and the other organisms present within it (Hutchinson 1957). For example, physiological temperature limitations may prevent a species from ranging into higher latitudes (Ungerer et al. 1999; Stillman and Somero 2000; Perry et al. 2005), while the presence of predators or competitors may restrict or shift its home range (Heithaus 2001; Heithaus and Dill 2002; de la Torre et al. 2017). Understanding distributions can help to identify not only where a species goes, but its abiotic requirements and the biotic interactions that drive its habitat use.

Understanding a population's distribution can be thought of as having two components, describing where individuals go and explaining why they go there. These goals are valuable on

their own, but together provide a far more comprehensive analysis of how animals use their habitat. The first component can be achieved via mapping occurrence data, but kernel density estimation from sighting data is best practice, and becoming more common (Worton 1989; Seaman and Powell 1996; Worton 1995). This approach is particularly useful for highly mobile animals which are not restricted to where they were sighted and travel between high-use areas. Areas of high occurrence can be indicative of core habitat or “hotspots” for the species (e.g. Hastie et al. 2004; Brough et al. 2019).

The second component mentioned above, to understand why animals use particular areas more than others, requires statistical modelling. Species Distribution Models (SDMs), also known as species habitat-models, comprise of a range of statistical techniques to investigate how the environment relates to a species’ distribution (Redfern et al. 2006). SDMs can be relatively simple, such as modelling the relationship of occurrence data against a potential environmental predictor. More complex models, however, are more usually employed, simultaneously modelling several predictors against the response (Guisan and Thuiller 2005). This allows a more robust and informative analysis, as the relative contribution of several predictors can be assessed. Often abiotic variables are used as predictors for SDMs, even though the drivers of distribution are likely to be a combination of abiotic and biotic interactions. Abiotic predictors (e.g. temperature) can have important direct effects on species’ distributions, are easier to measure and can act as proxies for biotic variables. Properly incorporating biotic variables, however, can increase the explanatory power of SDMs and provides a more realistic representation of what affects distribution. For these reasons incorporating biotic variables into models is becoming more common (e.g. Heithaus and Dill 2006; Torres et al. 2008)

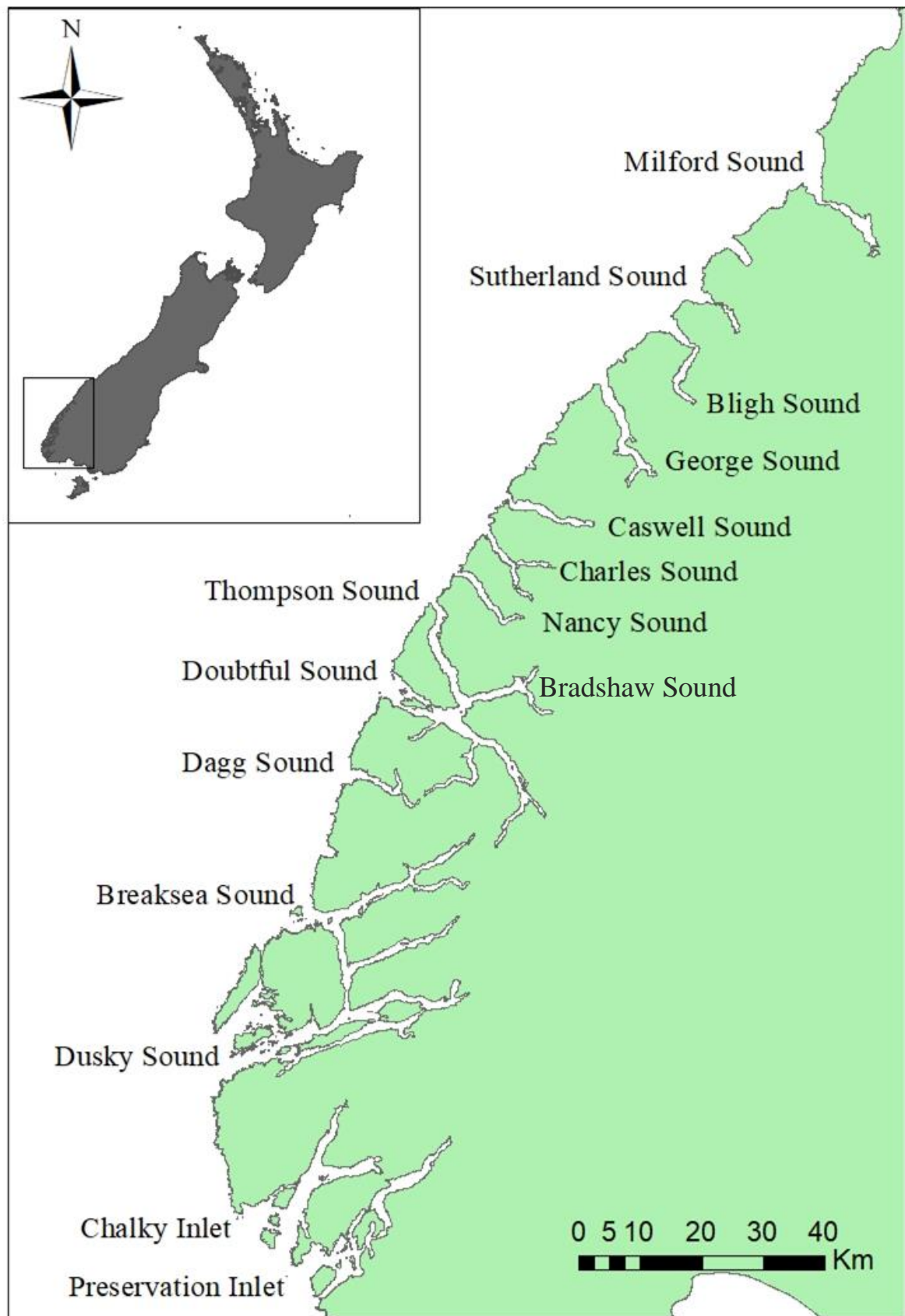
## **1.2 Study site**

### **1.2.1 Physical environment**

Situated on the south-west coast of the South Island of New Zealand is Fiordland National Park. Established in 1952, covering more than 1.2 million hectares, it is the largest terrestrial protected area in the country. As the name suggests, the Fiordland coastline consists of a series of large fjord systems, carved by glacial processes (Figure 1.1; Stanton and Pickard 1981). The fjords typically have very steep walls, and can reach depths over 400m (Stanton and Pickard 1981). Fiordland has large areas of old-growth native forest, steep terrestrial topography, hard

bedrock surfaces and very high rainfall. These all contribute to large freshwater and terrestrial inputs into the marine environment, driven by orographic rainfall and runoff (Stanton and Pickard 1981; McLeod and Wing 2007). Natural levels of freshwater input are sufficiently high that a low salinity layer (LSL), forms at the seawater surface (Gibbs 2001). The LSL is often stained brown due to tannins from the native forest, resulting in a dark surface layer which can limit light penetration. The high levels of freshwater input create strong gradients in both temperature and salinity (Stanton and Pickard 1981; Gibbs 2001).





**Figure 1.1.** The location of Fiordland National Park on the southwest coast of New Zealand with the position of all fjords.

### 1.2.2 Anthropogenic activity

Due to the large area of native forest and steep mountainous environment, access to the fjords is limited. There are only two roads leading into the fjords, one to Milford Sound and the other to Doubtful Sound; access to the road to Doubtful Sound is further limited due to needing to cross Lake Manapouri first. Despite this, the use of large vessels, helicopters and float planes means that all fjords are now subject to some level of anthropogenic activities. Fishing has occurred throughout Fiordland since prior to 1900, with both commercial and recreational operations restricted mainly by access (Guardians of Fiordland's Fisheries 1999). Following collapses of certain commercially fished species (e.g. rock lobster), fisheries protection measures were introduced in 1993 (Wing and Jack 2014). These protection measures were extended under the Fiordland Marine Management Act in 2005 to set up a network of MPAs, including no-take marine reserves.

Fiordland's large area of wilderness and dramatic scenery have stimulated the development of a substantial boat-based tourism industry. Although most tour operations are based in Milford and Doubtful Sounds, other nearby fjords, such as Dusky Sound, are also used. Tours include fishing, charter, scenery and wildlife viewing opportunities, and can occur on a daily basis (Lusseau and Higham 2004). Boat-based tourism increases the levels of noise pollution (Buckstaff 2004; Aguilar Soto et al. 2006; Guerra et al. 2014), can contribute to pressure on fish resources (for a review see Lewin et al. 2006), and has been shown to modify the behaviour of wildlife within the fjords (Lusseau 2003a, b; Lusseau and Higham 2004; Guerra et al. 2014).

The most significant anthropogenic impact in Fiordland is the hydroelectric power scheme in which water from Lake Manapouri flows via a tailrace into Doubtful Sound. The current resource consent allows for a discharge of up to  $550\text{m}^3\text{s}^{-1}$  of fresh water into Deep Cove, although the daily mean value is closer to  $400\text{m}^3\text{s}^{-1}$  (Greenaway 2009). The implementation of this power scheme tripled freshwater input into the head of the fjord (Gibbs 2001), resulted in a permanent LSL in Doubtful Sound, and fundamentally changed the ecology of the inner fjord (Boyle et al. 2001; Rutger and Wing 2006; Tallis et al. 2009; Jack et al. 2009).

### 1.2.3 Fieldwork locations

This study focuses on the fjord systems within the Doubtful/Thompson/Bradshaw and Dusky/Breaksea Sound complexes, hereafter referred to as Doubtful Sound and Dusky Sound, respectively. These are the two largest fjord areas within Fiordland, both of which extend

approximately 40km inland. Doubtful Sound has higher levels of anthropogenic activity, though both fjord systems are used for fishing and tourism purposes. Both fjord systems host separate, resident populations of bottlenose dolphins (*Tursiops truncatus*).

### **1.3 Study species: bottlenose dolphins (*Tursiops truncatus*)**

Bottlenose dolphins are the most comprehensively studied of all marine mammals (for reviews see Shane and Wells 1986; Kenny 1990; Wells and Scott 1999). They are long-lived, highly mobile predators with a global range that extends from temperate to tropical areas in both the southern and northern hemispheres (Moore 1953; Würsig and Würsig 1979; Wilson et al. 1997; Brough et al. 2015). Although predominantly coastal, this species has a flexible ecology and populations utilise a range of aquatic ecosystems; coastal, pelagic, estuarine, lagoons, rivers and even freshwater lakes (Duffield et al. 1983; Williams et al. 1993; Wells and Scott 1999). Typically these dolphins are highly social and group composition is based around fusion-fission dynamics in which individuals often move among groups (Shane and Wells 1986). Global population trends for bottlenose dolphins are difficult to ascertain due to the widespread distribution and potential contradictory trends in different populations (Wells and Scott 1999). When small populations are considered in isolation, however, several declines have been observed (e.g. Bejder et al. 2006; Currey et al. 2007; 2009a; Tezanos-Pinto et al. 2013).

#### **1.3.1. Bottlenose dolphins of Fiordland**

The bottlenose dolphins of Fiordland live near the southern-most extreme of the species' distribution (Bräger and Schneider 1998). There are three separate sub-populations of dolphins in Fiordland. The northern sub-population has the largest range, travelling among the seven northern fjords and regularly visiting Lake McKerrow (Lusseau 2005). They are the most difficult to access, and hence are the least studied. The sub-populations of Doubtful Sound and Dusky Sound are mostly resident (Williams et al. 1993; Schneider 1999; Currey et al. 2008), but have been reported to leave their respective fjords for short periods of time (Henderson et al. 2013).

The fjords are thought to present challenging conditions due to the cold water temperatures (Schneider 1999; Henderson et al. 2014). This is supported by the morphology of the dolphins, which is most similar to an offshore ecotype with small fins relative to body size (Schneider 1999). Calves are thought to be particularly at risk in this type of environment because they are thinly insulated (Henderson et al. 2014). Calving in Doubtful and Dusky Sounds is restricted

to the warmer months, which is thought to be another adaptation to the colder temperatures to protect the calves (Henderson et al. 2014). Compared to populations of bottlenose dolphins elsewhere, calf survival is low (Currey et al. 2009a; Henderson et al. 2014).

Both populations are small, and subject to regular long-term monitoring. The most recent abundance estimates are 68 (95% CI = 65-71) in Doubtful Sound, and 121 (95% CI = 120-122) in Dusky Sound (Johnston and Bennington 2018). Previous declines in abundance have led to Fiordland's bottlenose dolphins being listed as Endangered by the IUCN (Currey et al. 2007, 2009b). Research on population demographics began in Doubtful Sound in 1990 (Williams et al. 1993) and in Dusky Sound in 2007 (Currey et al. 2008). Regular monitoring has continued since, with at least three surveys occurring per year, creating a long-term database of sighting histories.

Bottlenose dolphins are generally described as opportunistic foragers (Wells and Scott 1999), consuming a wide variety of prey species, such as fish and cephalopods, based on availability (Santos et al. 2001; De Pierrepont et al. 2005). Limited dietary analyses have been completed for the dolphins of Fiordland, with stable isotopes indicating that the main prey source, in Doubtful Sound at least, was rocky reef associated fish (Lusseau and Wing 2006). There are a variety of reef associated fish commonly found in Fiordland including butterfly perch (*Caesioperca lepidoptera*), blue cod (*Parapercis colias*), tarakihi (*Nemadactylus macropterus*), sea perch (*Helicolenus percoides*) and spotty (*Notolabrus celidotus*; Francis 1996; Udy et al. 2019). The fish communities in Fiordland are also composed, however, of pelagic (e.g. arrow squid, *Nototodarus sloanii*, and mackerel, *Scomber australasicus* and *Trachurus declivis*), demersal (e.g. Hapuku, *Polyprion oxygeneios*), estuarine (e.g. sand flounder, *Rhombosolea plebeia*) and deep water species (e.g. rattail spp., *Caelorinchus spp.*; see Lusseau and Wing 2006) which may also be important for the dolphins diet.

### 1.3.2 Distribution of bottlenose dolphins in Doubtful and Dusky Sounds

Within Fiordland, habitat use by bottlenose dolphins varies both spatially and temporally, with high- and low-use areas which change seasonally (Schneider 1999; Elliott et al. 2011; Henderson 2013). In Doubtful Sound these changes were attributed to proximity to foraging areas (represented by distance to the fjord wall) and areas of warmer water temperature (Henderson 2013). Interestingly, these same patterns were not observed, or at least were not as obvious, in Dusky Sound (Henderson 2013). Areas that were consistently used for resting and socialising in Doubtful Sound were defined as “Critical Habitat” by Lusseau and Higham

(2004). Their research indicated that, although the frequency of occurrence in any one area may change seasonally, there was consistency in how the dolphins used these areas.

The previous analyses of dolphin distribution in Fiordland have included overlaying sightings on a grid and attempting to relate this to environmental conditions (Schneider 1999), comparing detection rates among nine acoustic monitoring sites (Elliott et al. 2011), and visual sightings analysed via Kernel Density Estimation and Mantel tests (Henderson 2013). All of these analyses attempted to relate the distribution of the dolphins in Doubtful Sound to environmental conditions, consistently finding that areas with higher sea surface temperature (SST) were correlated with higher use. Only Henderson (2013) investigated distribution of the dolphins in Dusky Sound. Although there were similarities to Doubtful Sound, SST did not seem to be as influential. All of these distribution analyses used data collected over relatively short time periods (i.e.  $\leq$  three years) and have been mainly descriptive. Furthermore, in no case has the role of biotic variables been investigated. For abiotic predictors such as temperature it is difficult to know whether any effect is direct, on the dolphins themselves, or indirect, acting on the distribution of prey (Henderson 2013).

### 1.3.3. Impacts on bottlenose dolphins in Fiordland

The Manapouri hydroelectric power scheme undoubtedly caused major ecological impacts in Doubtful Sound (Rutger & Wing 2006), but the lack of prior study prevents clear statements about effects on the dolphins. Currey et al. (2009a, b) drew attention to the co-occurrence of the establishment of the second tailrace tunnel in 2002 and a significant decline in calf survival rate. In addition, exposure to freshwater is thought to be related to high incidence of epidermal disease (Rowe et al. 2010). The main current impacts on the dolphins, however, are thought to stem from the ecotourism industry (Lusseau & Higham 2004; Guerra et al. 2014). Although dolphin watching is not the principal focus of the ecotourism companies in Fiordland, the dolphins are certainly a drawcard (Lusseau and Higham 2004). For example, many companies use images of dolphins on their websites and other advertising material. Vessel activities can cause short-term changes to the behavioural state of a dolphin group, including lower group cohesion, avoidance, greater rate of and more variable vocalisations, and decreases in resting behaviours (e.g. Bejder et al. 1999; Constantine et al. 2004; Guerra et al. 2014). Longer term impacts have also been reported, through area avoidance and declines in abundance (Lusseau 2005; Bejder et al. 2006). The Doubtful Sound population is currently most at risk to these

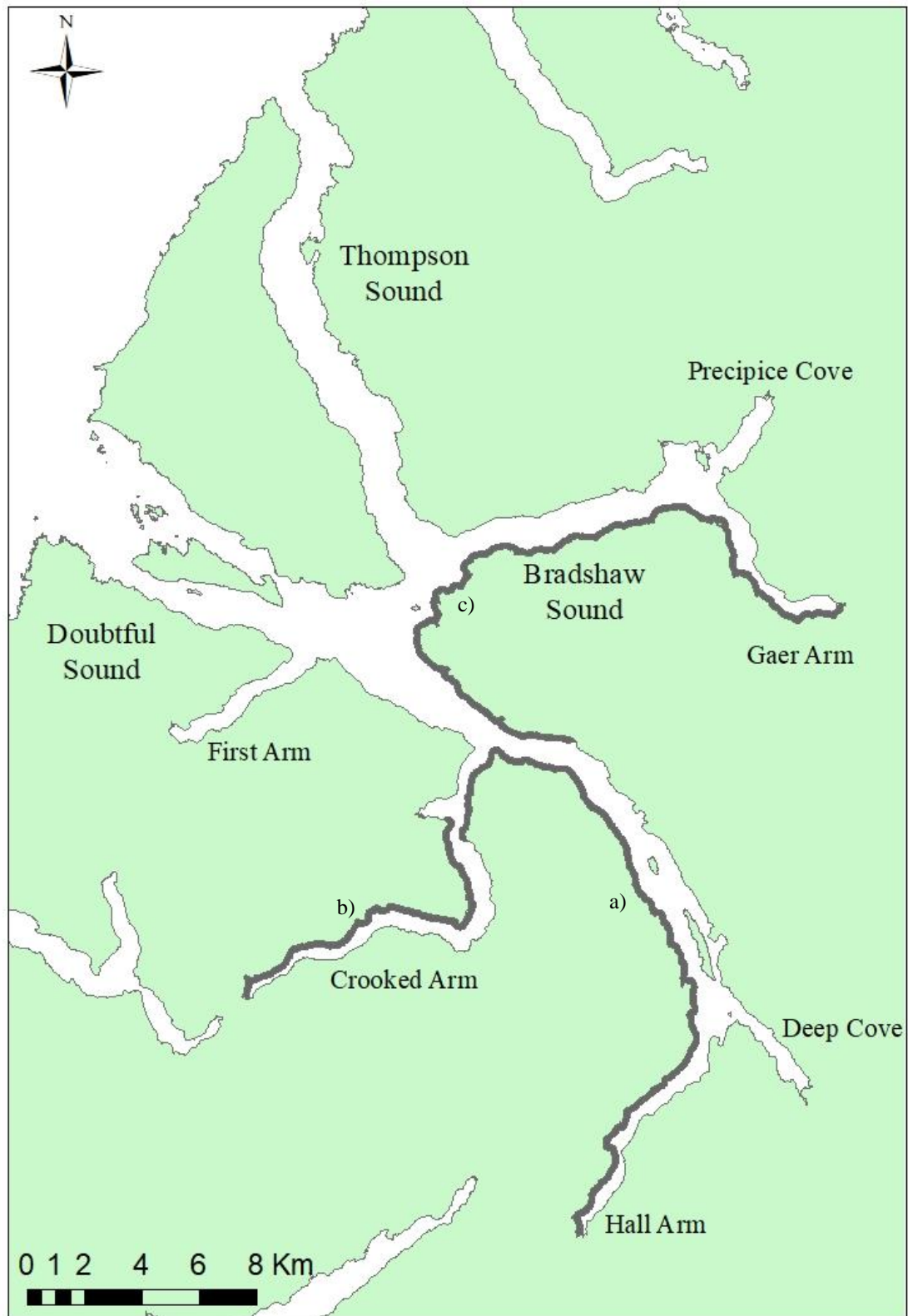
impacts, due to the high residency of the dolphin population and higher relative tourism pressure.

## **1.4 Management**

Marine mammals in New Zealand are protected under the Marine Mammal Protection Act (1978) and Marine Mammal Protection Regulations (1992). These acts, in addition to protecting marine mammals from harassment, disturbance, injury or death, control vessel behaviour around the animals. Vessels are supposed to approach from behind or beside a dolphin group, travel at no-wake speeds (below 5 knots) within 300m, not cut through or circle a group, and travel slowly when departing the animals. Swimming with dolphins is permitted if no young animals are present.

In response to declines in abundance of bottlenose dolphins in Doubtful Sound (Currey et al. 2009a, b), additional management measures were introduced under a voluntary Code of Management (COM; Department of Conservation 2008). This restricts tour vessel behaviour around the dolphins, including no radio communication about dolphins and no deviation from the predetermined route. These measures aimed to reduce encounters and allow any interaction with vessels to be on the dolphins' terms. Additionally a spatial management system was initiated in Doubtful Sound through the establishment of Dolphin Protection Zones (DPZs; Figure 1.2). The locations of these were loosely based on the critical habitat defined by Lusseau & Higham (2004), with the resulting DPZs consisting of three areas that extend 200m from the fjord wall. Because the COM is voluntary it relies on operators to agree to the terms. Other fjord users are not necessarily aware of the COM. To resolve this issue there is ongoing communication and education for fjord users, such as SMART (Sustainable Marine Mammal Actions in Recreation and Tourism) courses from the Department of Conservation (DOC), along with pamphlets and signage. Dusky Sound has no additional conservation management.

The DPZs within Doubtful Sound were established in 2008, however, there has been no quantitative evaluation of their effectiveness for the dolphins. Therefore, there is a need to investigate whether DPZs still protect important dolphin habitat, or whether their location and extent need to be adjusted to better suit current distribution and habitat use.



**Figure 1.2.** Location of Dolphin Protection Zones represented in dark grey in Doubtful Sound with specific place names included. DPZs are named as a) Hall Arm to Crooked Arm, b) Crooked Arm and, c) Bradshaw Sound.

## **1.5 Thesis objectives**

The primary aim of this thesis is to investigate the habitat use of bottlenose dolphins in Fiordland. In addition to increasing our knowledge about the ecology of these dolphins, I wanted to assess the utility of the spatial management that has been implemented in Doubtful Sound and the potential of this approach in Dusky Sound. Without formal assessment, the actions of conservation management must rely on what amounts to acts of faith for their continued justification (Dawson and Slooten 1993). DPZs were established over 10 years ago in Doubtful Sound based on research completed over 15 years ago. There is therefore a pressing need to assess whether this management action is still appropriate. Similarities between the bottlenose dolphin populations in Doubtful and Dusky Sounds mean that there may be a need to extend protection into Dusky Sound, if trends in tourism continue to increase in this fjord.

My specific research goals are:

1. To describe past and present habitat use by bottlenose dolphins in Doubtful and Dusky Sounds, and investigate changes over time and between seasons.
2. To provide a quantitative analysis of the abiotic factors influencing the habitat use of bottlenose dolphins in Doubtful and Dusky Sounds.
3. To investigate the role that biotic factors have on the habitat use of bottlenose dolphins in Doubtful Sound.

Each specific goal for this thesis is presented in a different chapter and written in the form of an individual manuscript. This is because each goal has a unique set of methods. The combined results of this thesis are used to give an overall assessment of habitat use by the bottlenose dolphin populations in Doubtful and Dusky Sound, assess current spatial management in Doubtful Sound, and provide a recommendation for potential areas of protection in Dusky Sound.

### **Statement about the data used for this thesis**

Parts of this thesis involve analysis of a long-term data series on the bottlenose dolphins of Fiordland that extends back to 2005. I began data collection in 2017 and collected all data in 2018, including those on potential prey. Data prior to this were collected by Rohan Currey, Lucy Rowe, Shaun Henderson, Tom Brough and David Johnston, all under the supervision of Steve Dawson, Liz Slooten and, since 2010, Will Rayment.



## Chapter 2

### Distribution of bottlenose dolphins in Doubtful and Dusky Sounds revealed by kernel density estimation

#### 2.1 Introduction

Accurate descriptions of the distribution of a species or population can help to identify ecological links, and elucidate that species' role in the environment (Heymann et al. 2017). Examining how this overlaps with the distributions of other species can reveal biotic interactions such as competition (Pimm and Rosenzweig 1981; Koehler and Hornocker 1991; Nicholls and Racey 2006), mutualism (Heymann et al. 2017) and predation (Heithaus and Dill 2002). Describing a species' distribution also helps us to understand or identify the environmental factors which limit its range (Stramma et al. 2012; Scales et al. 2015). Essentially, understanding a species' distribution reveals how a species uses available habitat and provides insight into which habitat is critical for the species' survival. This knowledge can then be used to protect threatened species via spatial management, such as marine or land-based reserves (Agardy 1994). Such areas may aim to reduce potential threats such as fishing (e.g. Jack et al. 2009), tourism pressure (e.g. Lusseau and Higham 2004), or facilitate risk assessment (e.g. from plastic pollution; Darmon et al. 2017). North Atlantic right whales (*Eubalaena glacialis*) provide a good example. Boat-strike is a major anthropogenic threat in areas where shipping routes and critical habitat overlap. The introduction of specific rules targeting vessel speeds in key areas, however, has resulted in significant declines in mortality of whales from interactions with vessels (Laist et al. 2014; van der Hoop et al. 2015).

Human interests, such as economic, recreational or cultural factors, often influence how spatial management is implemented, resulting in less effective protection for the target species. For example, protection of Hector's dolphin (*Cephalorhynchus hectori*) from bycatch in gill netting covers only the inshore portion of the dolphins' range; projected population trends suggest that current protection is unlikely to result in recovery of the species (Slooten and Dawson 2010). Likewise, for the example of right whales given above, the managed areas do not extend to the migratory corridors, and vessel strikes still occur (Laist et al. 2014). Furthermore, entanglement in fishing gear, another major cause of mortality, is not targeted by these management actions (Kraus et al. 2016).

Large predatory species are important in the ecosystem because they are often charismatic and can be keystone species that have a disproportionate effect on the environment (Estes and

Palmisano 1974; Mills et al. 1993; Estes 1994). Also, conservation of charismatic species, such as dolphins, often receives public support despite other human interests (Ducarme et al. 2013), making these species easier targets for protection. Determining effective spatial management, however, presents special challenges, as large predators are often highly mobile and long-lived (Redfern et al. 2006). Large ranges can extend into multiple ecosystems (McCauley et al. 2012) or beyond national borders, and migratory pathways may not be represented (Runge et al. 2014). There is an additional challenge that highly-mobile, long-lived species may shift their habitat use in response to environmental changes, or human impacts (Redfern et al. 2006), compromising spatial management of a fixed area (Wilson et al. 2004; Hartel et al. 2015).

The bottlenose dolphins (*Tursiops truncatus*) of Doubtful and Dusky Sounds comprise of two small populations that show high site fidelity to their respective fjords (Williams et al. 1993; Schneider 1999; Currey et al. 2008). Previous research on the distribution and habitat use of these dolphins has incorporated data recorded over a maximum of three years. The analyses have included log-likelihood tests (Schneider 1999), behavioural analysis (Lusseau and Higham 2004), spatial analysis of acoustic detections (Elliott et al. 2011), and Kernel Density Estimation of visual sightings (KDE; Henderson 2013). These studies revealed variation and seasonal shifts in habitat use within the fjords (Schneider 1999; Elliot et al. 2011; Henderson 2013). Additionally, research on habitat use has been important in defining appropriate areas for spatial management in Doubtful Sound (Lusseau and Higham 2004).

Tourism traffic has been highlighted as one of the main anthropogenic impacts to the dolphins in Doubtful Sound (Lusseau 2003a, b, 2006), and is becoming more prevalent in Dusky Sound. Three areas within Doubtful Sound were designated as Dolphin Protection Zones (DPZs) in 2008. Each DPZ is a 200m wide strip at the edge of the fjord designed to reduce chance encounters between vessels and the dolphins within critical habitat (Department of Conservation 2008). Current management in Doubtful Sound, based on research completed 15 years ago (Lusseau and Higham 2004), might no longer be appropriate if the dolphins have shifted their habitat use. To ensure that management remains effective, there is a need to investigate current distribution of the bottlenose dolphins in Doubtful Sound.

This chapter aims to quantitatively describe the habitat use of bottlenose dolphins in Doubtful and Dusky Sounds. To achieve this I used the largest available datasets and most up-to-date analysis methods. I used sighting information data from 2005 to 2018 (Doubtful Sound) and 2009 to 2018 (Dusky Sound) to investigate potential changes in distribution over time and to

update analyses of seasonal patterns in habitat use. Previous research indicated that dolphins shifted their distribution away from the inner fjord during winter (Schneider 1999; Henderson 2013). Although Henderson (2013) found similar results to Schneider in a study completed over ten years later, there has been no formal analysis investigating changes in distributions over time. Furthermore, in recent years the bottlenose dolphins of Doubtful Sound have been recorded leaving the fjord for extended periods (Henderson et al. 2013); a trend that appears to be increasing in frequency (pers. obs.). If the dolphins are extending their range it may indicate that, for the Doubtful Sound population at least, environmental conditions, anthropogenic pressure or food availability have changed.

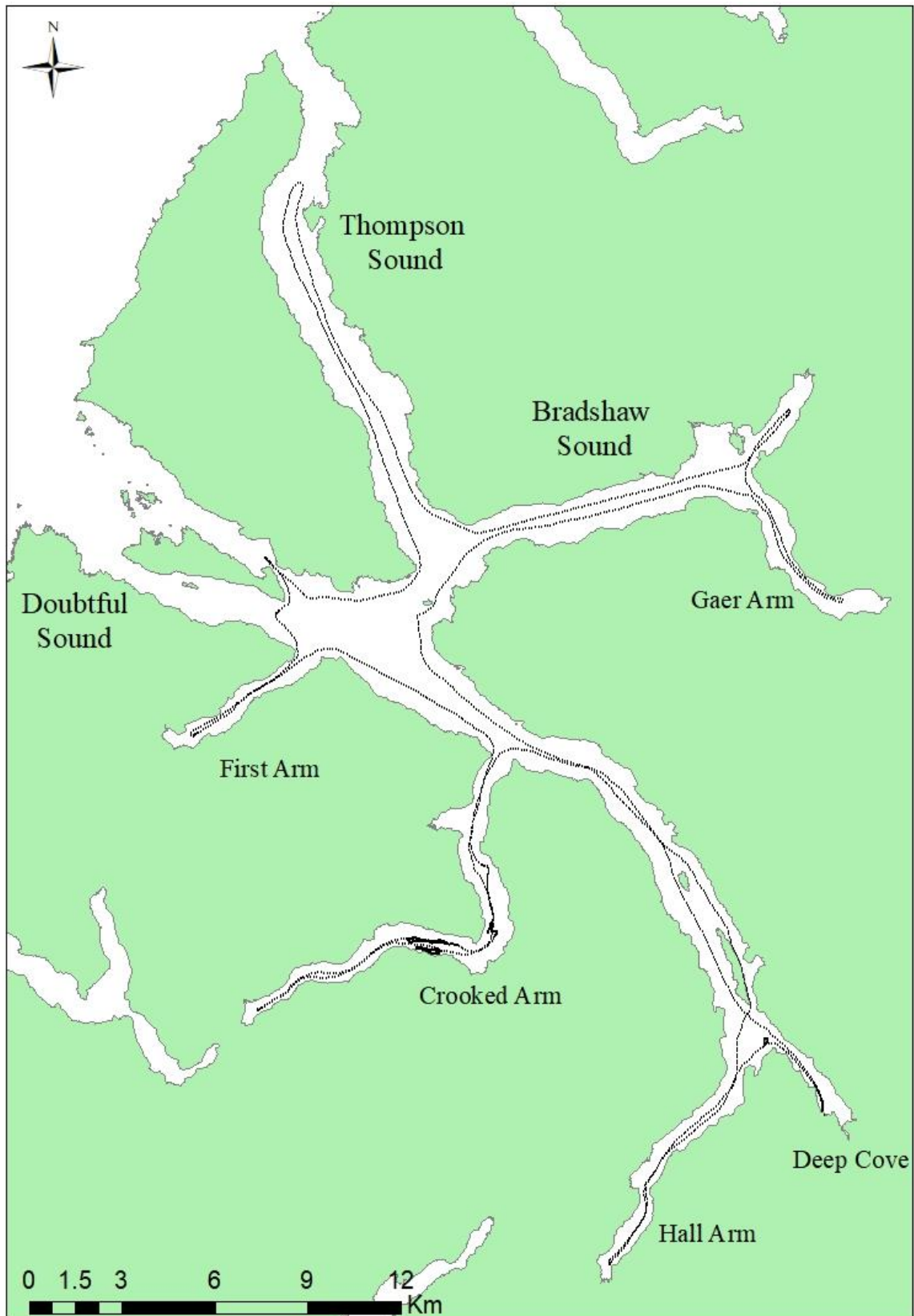
## **2.2 Methods**

### **2.2.1 General Field Methods**

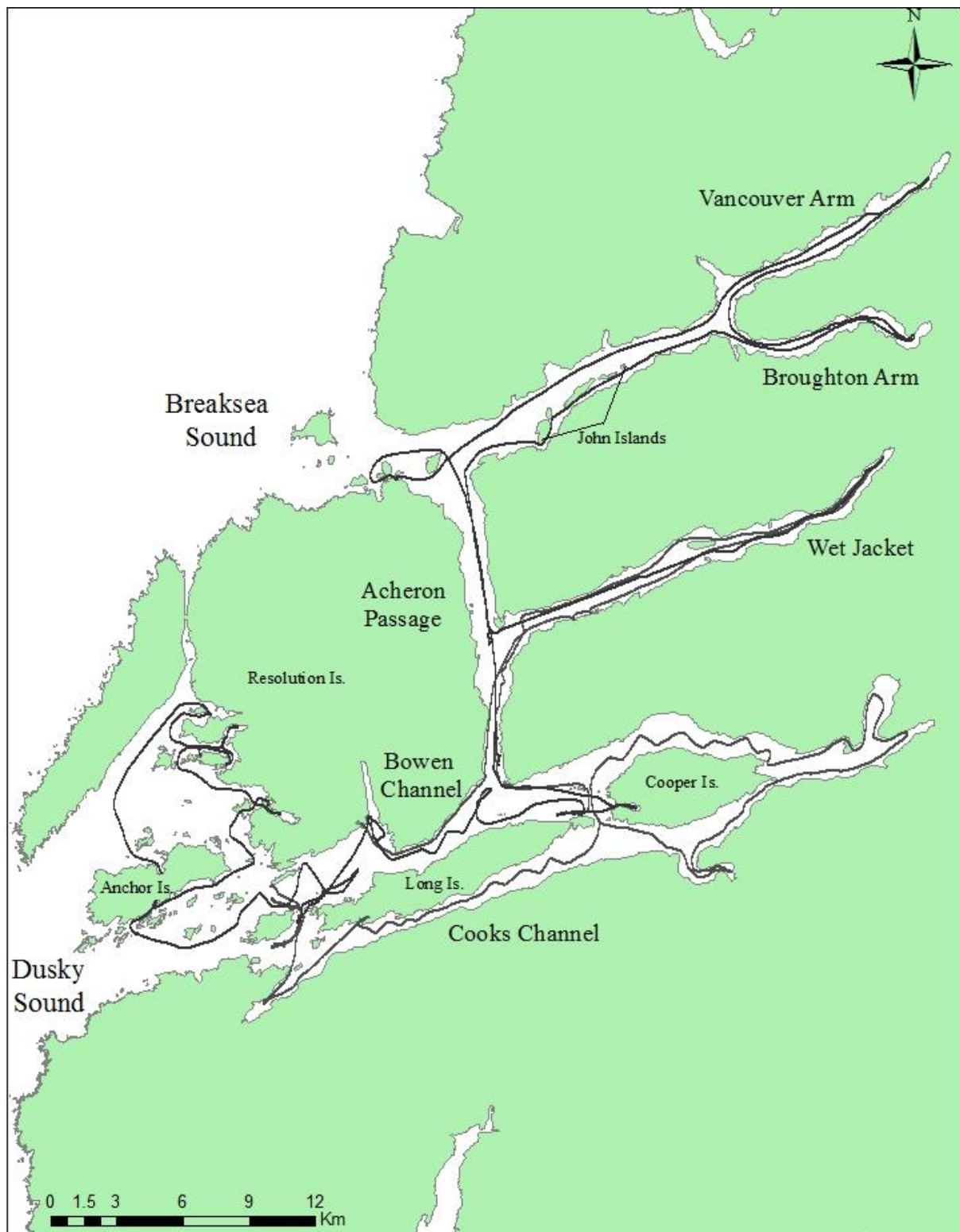
Monitoring of the bottlenose dolphin populations has been conducted by the Marine Mammal Research Group at Otago University since 1990 in Doubtful Sound, and 2007 in Dusky Sound, with collaboration from the Department of Conservation since 2007. Monitoring trips occurred at least three times per year during summer/autumn, winter and spring, with additional research trips in Doubtful Sound for student research projects. The long-term focus of the project has been gathering photo-ID data to assess population parameters, broadly following fieldwork protocols established by Schneider (1999). This means that the long-term dataset contains information on group composition, sighting locations and survey effort which can be used to investigate distribution.

Surveys were conducted along a standardised survey route (Figure 2.1, 2.2; Schneider 1999) from a 5m aluminium research vessel (RV) using a 60 or 70hp four stroke outboard engine, or sometimes from a 5.5m RV using a 115hp four stroke outboard engine. Surveys were conducted on all possible days, weather permitting, over a one to four-week period, depending on the research question being addressed. Long-term monitoring trips were between five and 30 days in Doubtful Sound, and eight to 15 days in Dusky Sound. When dolphins were sighted, the RV left the survey route and approached, following NZ Marine Mammal Protection Regulations (1992). Researchers photographed dorsal fins to record which individuals were present, giving equal effort to marked and unmarked dolphins. The RV remained with the group of dolphins until researchers believed they had photographed all individuals in the group (Henderson 2013), or, on rare occasions, when the dolphins showed signs of avoidance.

We recorded the location, time of sighting, estimate of group size and number of calves in the group, as well as the group's behavioural state (every fifteen minutes). When the encounter was over, the RV returned to the survey track to continue surveying the fjord, until a new group was sighted, or the survey finished for that day. Logs of the survey route were recorded using GPS tracking from a variety of GPS recording devices; the location of the RV was recorded every one, 20 or 60 seconds, depending on the trip.



**Figure 2.1.** Example survey route in Doubtful Sound. Survey track is actual GPS locations taken on board the research vessel Nemo over one day.



**Figure 2.2.** Example survey route in Dusky Sound. Survey track is actual GPS locations taken on board the research vessel Nemo over two days.

### 2.2.2 Kernel Density Estimation

To investigate the distribution and core habitat of a species, population or individual, a range of methods are available, including the minimum convex polygon (Mohr 1947), harmonic mean (Dixon and Chapman 1980), bivariate normal models (Jennrich and Turner 1969; Koepl et al. 1975), Fourier series (Anderson 1982) and kernel density estimation (KDE; Worton 1989). KDE takes a non-parametric approach to describing habitat use, meaning they are not restricted to linear relationships and can provide accurate density estimates of any shape. This is ideal for areas such as Fiordland because of the highly convoluted coastline, and for the bottlenose dolphins as their habitat use has been shown to vary within the fjord system (Henderson 2013). KDE essentially provides an estimate of the probability of observing individuals or groups at any point within the given distribution (Silverman 1986; Seaman and Powell 1996). The method outperforms other methods for describing home ranges (Worton 1989, 1995), and is commonly used in ecology (Gutowsky et al. 2015; Scales et al. 2015; Darmon et al. 2017; Heymann et al. 2017), and for cetaceans in particular (Heide-Jorgensen et al. 2002; Rayment et al. 2009; Sveegaard et al. 2011; Henderson 2013). For these reasons, I have chosen to use KDE to describe habitat use of the dolphins in Doubtful and Dusky Sounds.

#### *Location information*

I used data from the long-term dataset collected between 2005 and 2018 in Doubtful Sound, and 2009 and 2018 in Dusky Sound. In Doubtful Sound these years encompass a time before spatial management was established (2008) and are continuous to the latest data available. In Dusky Sound these years range from the earliest consistent data available to the latest.

Dolphin group locations were generated from survey tracks. The principal purpose of the surveys is photo-ID and therefore the RV can spend extended periods with one group (up to two hours; Henderson 2013). Although the RV has been shown to have minimal impacts on the behaviour of the dolphins (Guerra et al. 2014), to minimise any effect on distribution I used the location of the dolphin group at time of first approach. Each group location was estimated by interpolating the RV's position at the time the first photo-ID image was taken (typically within 20m of the dolphin group) using the GPS track-log.

Using groups instead of individuals allows KDEs to be produced for the population as a whole, and allows for changes over time of individuals within the population. Because the bottlenose

dolphin population in Doubtful Sound is normally separate from the population in Dusky Sound (Henderson et al. 2013), these two populations were modelled separately.

Seasonal and temporal habitat use was investigated by partitioning the location data. For the Doubtful Sound analysis, seasons were defined as summer (Dec-Feb), autumn (Mar-May), winter (Jun-Aug) and spring (Sept-Nov). In Dusky Sound, there have traditionally been only three monitoring trips per year, with the “summer” trip occurring between late February and May. Therefore, for the Dusky Sound analysis autumn and summer months were combined into one season, referred to as summer hereafter, while winter and spring months were consistent with those used in Doubtful Sound.

The data were also partitioned for a longitudinal investigation of changes in habitat use. To ensure there were enough sightings to describe habitat use within the dolphins’ range, periods of three to four years were combined. This length of time was consistent with time periods used in previous studies (Schneider 1999; Lusseau and Higham 2004; Henderson 2013). For the Doubtful Sound analysis, four time periods were used: from 2005-2008 (prior to the establishment of DPZs), 2009-2011, 2012-2015 and 2016-2018. The time periods were similar for Dusky Sound, except only the three later periods were used, as data between 2005 and 2008 were not available for this study.

Spatial autocorrelation is always a concern in spatial analyses, because where an animal goes next is highly dependent on where it was last (Swihart and Slade 1985). One strategy to reduce autocorrelation is to separate sightings temporally, giving enough time between sightings to allow for the study species to access any area in their range before the next sighting is made. If we assume an average swimming speed for bottlenose dolphins of  $6.1\text{km.h}^{-1}$  (Würsig and Würsig 1979; Williams et al. 1992) the dolphins would be capable of travelling between the most distant parts of the fjord in eight hours (Doubtful Sound) and 11 hours (Dusky Sound), respective distances of 49km and 67km. I assumed, therefore, that bottlenose dolphin groups sighted on separate days were spatially independent. Photo-ID data were used to determine if multiple groups sighted on the same day were separate; if a dolphin group had any members from a previous sighting that day, it was excluded from further analyses.



### *Analyses*

I generated separate Kernel Density Estimates (KDEs) for Doubtful and Dusky Sounds with ArcMap v.10.6.1 (ESRI; Environmental Systems Research Institute, Redlands, California, USA ) using the “Home Ranges With Barriers” tool in the “Home Range Tools” toolbox (MacLeod 2013). The use of this tool avoids interpolating location points across land features, depending on the value of the smoothing parameter (also referred to as bandwidth or  $H$ -value). This means that density estimates in areas such as Crooked Arm, should reflect the sightings in Crooked Arm, and not include sightings from areas that are spatially close but separated by land, e.g. Hall Arm. KDEs produce a density raster, and 95 and 50 Percent Volume Contours (PVC). The PVCs represent increments of space use by the population, i.e. the 95PVC defines the area containing the top 95% of the density estimate, and can be interpreted as the limits within which the population spends 95% of its time. The 95PVC was used to approximate the total range of the population, and the 50PVC was used to represent the core habitat (e.g. Rayment et al. 2009).

The KDE and PVCs are the result of interactions between the smoothing parameter and cell size (i.e. the density estimate over a defined area). The accuracy of KDEs is dependent on two main factors, the independence of datapoints and the value of the smoothing parameter ( $H$ , Worton 1989; Seaman and Powell 1996; Gitzen et al. 2006; Kie 2013). Choice of smoothing parameter is considered more important, because it has the greatest influence on the outcome. When  $H$  is set too high, density estimates will be over-smoothed, potentially losing fine-scale variation in habitat use. When set too low, the resulting density surface will appear fragmented and have inflated estimates at each data point (Fieberg 2007; Kie 2013). I followed the rule-based approach described by Kie (2013), of using the lowest bandwidth, where possible, that did not fragment the 95PVC. This method allows for a smoothing parameter that represents connectivity within the home range, and has been applied to a wide range of ecological studies (Hernandez-Blanco et al. 2015; Sólmundsson et al. 2015; Fetterplace et al. 2016; Wells et al. 2017; de la Torre et al. 2017). When making comparisons among different datasets (i.e. among seasons or time periods), however, it is important to keep parameters consistent so that differences in the density estimates are solely due to the data. Therefore, so seasons or time periods could be compared, cell size was kept the same and I used the lowest smoothing parameter that did not fragment the 95PVC in any of the comparison datasets. For the seasonal analysis in Doubtful Sound cell size was  $200\text{m}^2$  and the smoothing parameter was 10,000m; in Dusky Sound cell size was  $300\text{m}^2$  and the smoothing parameter was 14,100m. For the

longitudinal analysis in Doubtful Sound cell size was 200m<sup>2</sup> and the smoothing parameter was 7400m; in Dusky Sound cell size was 300m<sup>2</sup> and the smoothing parameter was 12,300m.

### *Weighting locations*

Survey effort throughout the fjords was not uniform. For example, in Dusky Sound it takes at least two days to cover the entire fjord, and weather is a constraining factor limiting ability to survey parts of both fjords. To adjust for this all sightings were weighted by 1/survey effort. I sectioned the fjords into 49 zones in Doubtful Sound, and 97 in Dusky Sound. Zones were approximately one kilometre by four kilometres in size, and defined using geographic features (Appendix 1; 2). Each zone was weighted for survey effort, determined as:

$$E_{ij} = \frac{S_j}{S_{ij}}$$

Where  $E_{ij}$  is the inverse measure of relative effort for zone  $i$  in period (time period or season)  $j$ , calculated by dividing the total number of surveys  $S$  in period  $j$ , by the number of surveys  $S$  to zone  $i$  in period  $j$ . All presence locations were assigned with the corresponding weighted survey effort of the zone they were sighted in. This calculation was applied to all subsets of data investigated.

Groups of all sizes (ranging from one individual to >80) were included in this study, so the effect of group size needs to be accounted for. This is because an area used by many individuals is likely to be more important than an area being used by only one or two, and therefore should have a greater effect on the final density estimates. Due to high sampling intensity in Doubtful and Dusky Sounds, temporary marks on the dolphins' dorsal fins could be used to identify all individuals in the population (Currey et al. 2007; Johnston et al. 2017). The number of individuals identified by photo-ID in each group was therefore used as an estimate of group size. To account for group size in the KDE, I used the number of individuals in each group as a proportion of the total number of individuals sighted within that period (i.e. time period or seasons) to weigh each location point.

The final weight ( $w$ ) of each location point ( $x$ ) was therefore calculated as:

$$w_x = E_{ij} \times \frac{g_{sx}}{n_j}$$

Where  $E_{ij}$  is the effort ( $E$ ) of area  $i$  at period (time period or seasons)  $j$ ,  $gs_x$  is estimated group size ( $gs$ ) for location point  $x$  and  $n_j$  is the total number of dolphins sighted ( $n$ ) in period  $j$ .

#### *Analysis of core habitat overlap*

To investigate the similarities and differences in habitat use between time periods or seasons, I quantified the overlap of core habitat (50PVC). Total 50PVC area was measured for each KDE using the ArcMap v.10.6.1 “add geometry attributes” tool. Percentage area overlap (required for comparisons among time-periods and seasons) was calculated as:

$$\% \text{ overlap} = \frac{50PVC_{a,b}}{50PVC_a + 50PVC_b - 50PVC_{a,b}} \times 100$$

Where  $50PVC_a$  is the area of the core habitat from one period (time period or season),  $50PVC_b$  is the area of the core habitat from a comparison period and  $50PVC_{a,b}$  is the area of the overlap between core habitat  $a$  and  $b$ . This method provides a direct quantitative comparison of how similar or distinct 50PVC areas are (e.g. Guerra et al. 2018).

The area overlap between core habitat (50PVC) and the DPZs in Doubtful Sound was also investigated. This was completed using the same equation as described above, except the area of each DPZ, and the collective area of all DPZs was substituted for  $50PVC_b$ . ArcMap v.10.6.1 was used to measure DPZ, core habitat and overlap areas, for each season and time period.

## 2.3 Results

Between 2005 and 2018 in Doubtful Sound 408 surveys were conducted and 432 independent sightings of bottlenose dolphin groups were made (Table 2.1). In Dusky Sound, between 2009 and 2018, 278 surveys were conducted, and 372 independent sightings of bottlenose dolphin groups were made (Table 2.1). Seasonally, the highest sighting rate occurred during summer and the lowest during spring, in both Doubtful and Dusky Sounds. Although in Doubtful Sound autumn, winter and spring sighting rates were all relatively similar (within 0.05). Sighting rate has slightly decreased over time in Doubtful Sound, with the highest number of relative sightings occurring in the earliest time period (2005-2008), and the least in the latest (2016-2018). In Dusky Sound the earliest time period (2009-2011) also had the most sightings, but the middle and later time periods were similar.

**Table 2.1.** Sightings of bottlenose dolphin groups and survey effort in Doubtful Sound and Dusky Sound for different time periods and seasons. Dashes indicate that no associated data were available.

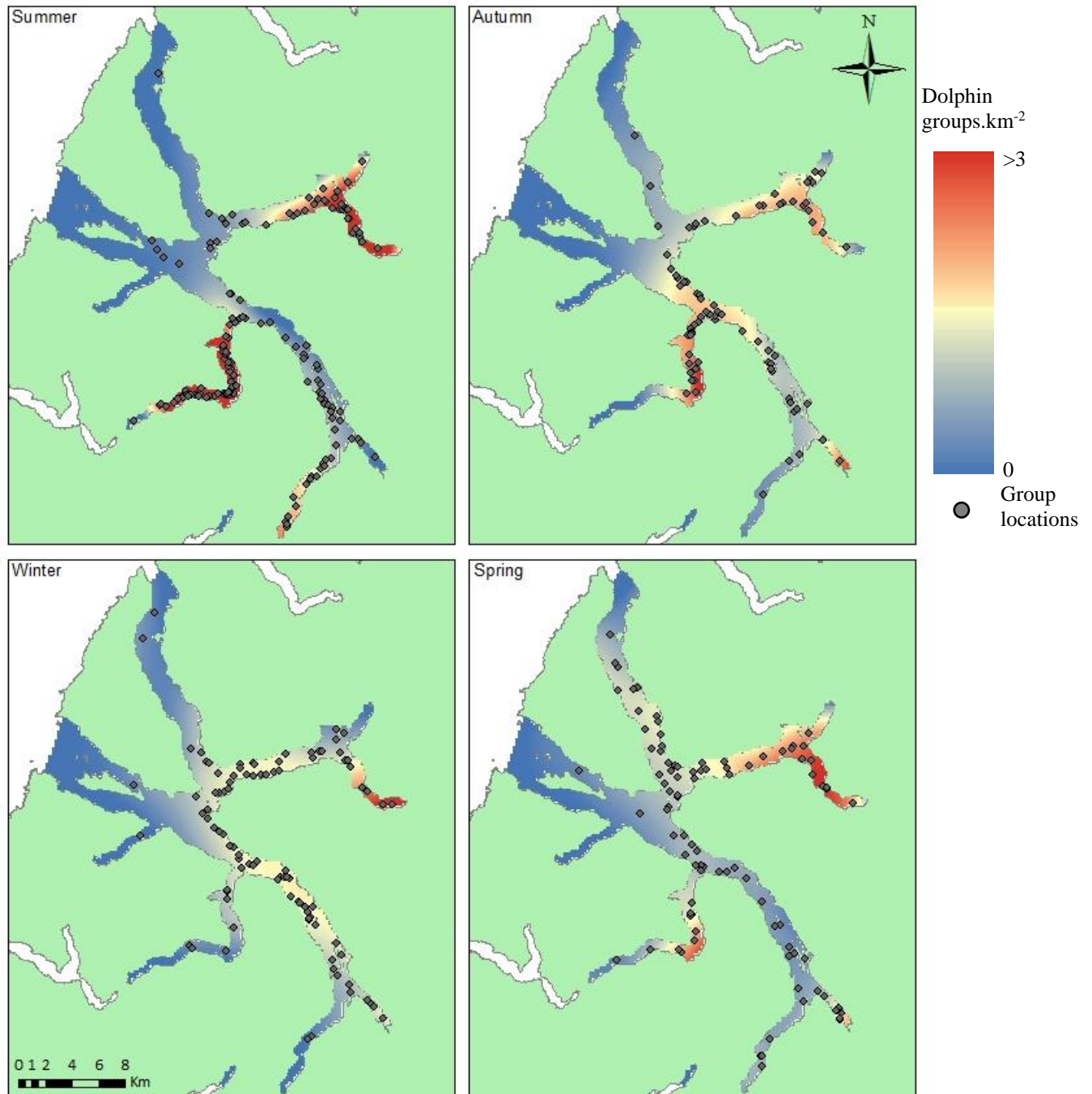
Data Partitioning	Doubtful Sound sightings	# of surveys Doubtful Sound	Doubtful Sound sightings/survey	Dusky Sound sightings	# of surveys Dusky Sound	Dusky Sound sightings/survey
Summer	161	138	1.17	133	89	1.49
Autumn	83	82	1.01	-	-	-
Winter	94	92	1.03	137	96	1.43
Spring	94	96	0.98	102	83	1.23
2005-2008	157	128	1.23	-	-	-
2009-2011	86	83	1.04	133	87	1.53
2012-2015	106	107	0.99	139	107	1.30
2016-2018	83	90	0.92	100	74	1.35

### 2.3.1 Doubtful Sound

#### *Seasonal distribution analysis*

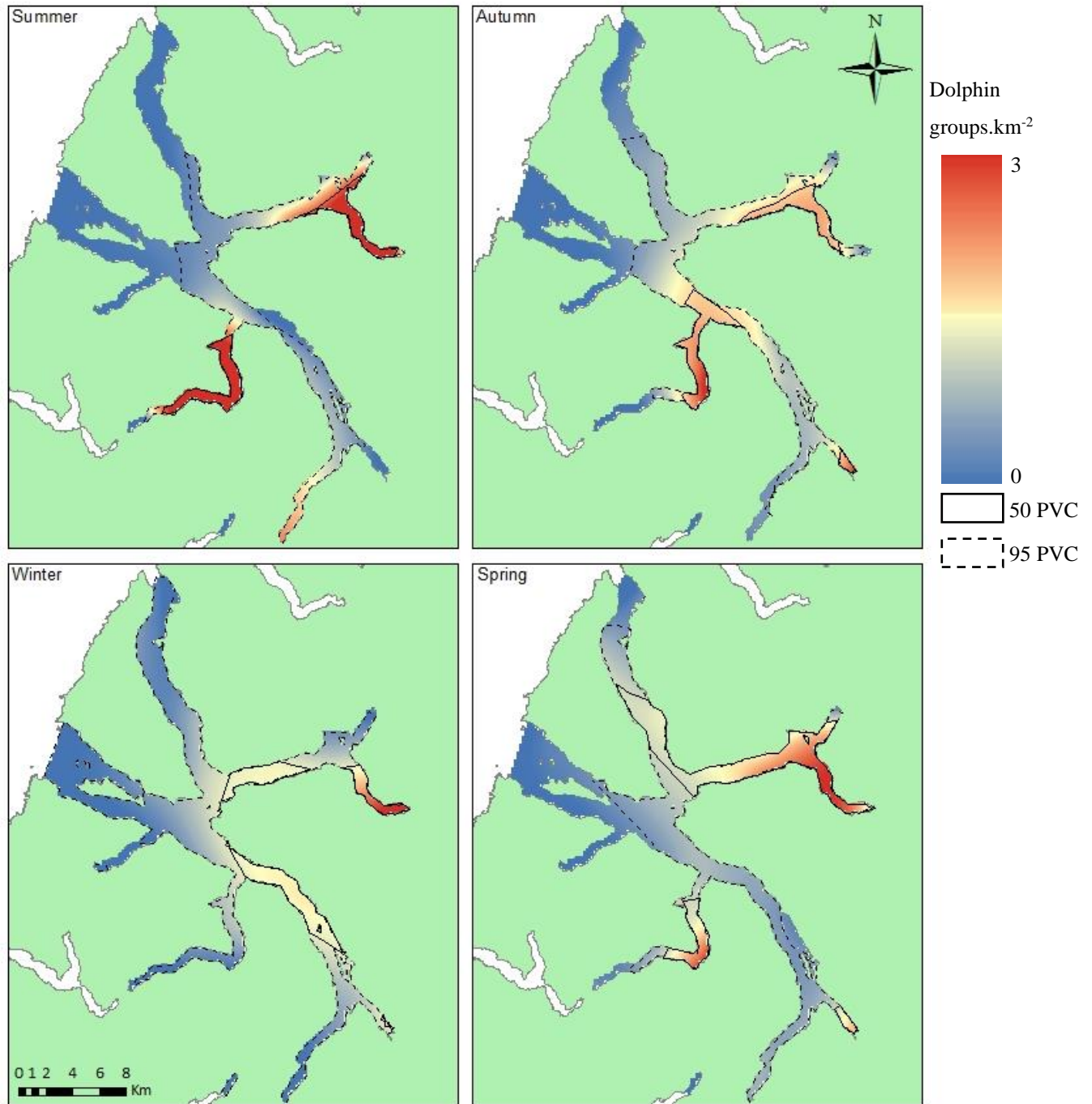
Group sighting locations in Doubtful Sound, partitioned by season, showed far fewer sightings in Crooked Arm during winter than in other seasons and more dispersed sightings in spring (Figure 2.3). Summer and autumn showed a concentration of sightings in Crooked Arm and the northeast end of Bradshaw Sound. Although there was variation in the location and frequency of dolphin sightings between seasons, Bradshaw Sound and the inner main area in Doubtful Sound were used consistently year round. Areas with a greater number of sightings

generally reflected higher density estimates; an exception to this is the inner main channel in Doubtful Sound during summer and spring.



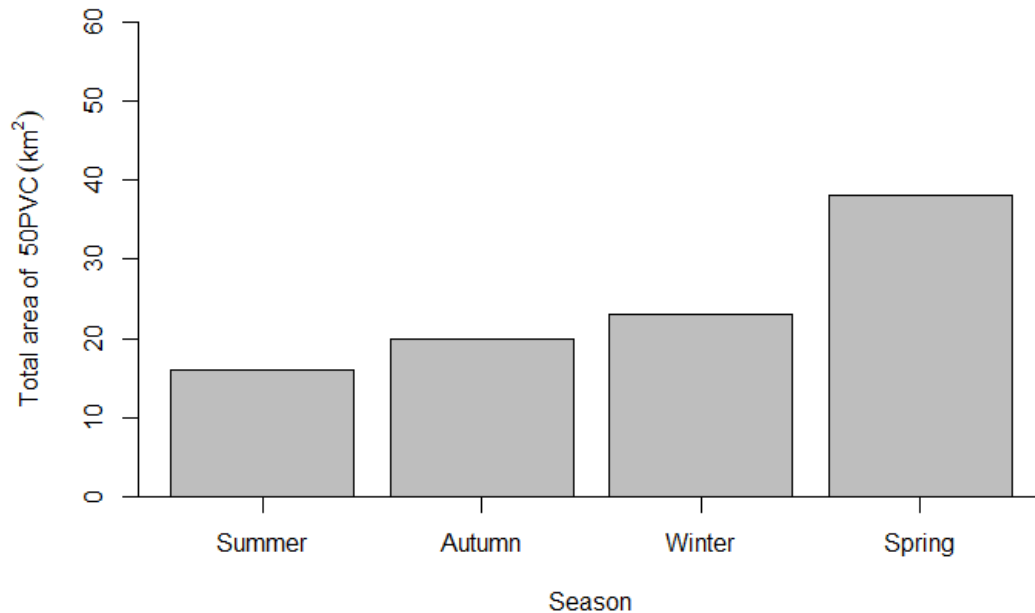
**Figure 2.3.** Seasonal bottlenose dolphin group locations in Doubtful Sound between 2005 and 2018: summer (n=161 sightings), autumn (n=83), winter (n=94) and spring (n=94). Sightings are superimposed on seasonal kernel density estimates (h-value = 10000m, cell size = 200m<sup>2</sup>). Colours indicate relative density; hot colours are higher densities and cold colours are lower densities.

Bottlenose dolphin core habitat, as estimated by 50PVC, showed broadly consistent use of habitat, the main exceptions being the abandonment of Crooked arm in winter, and frequent use of Deep Cove in autumn and spring (Figure 2.4).

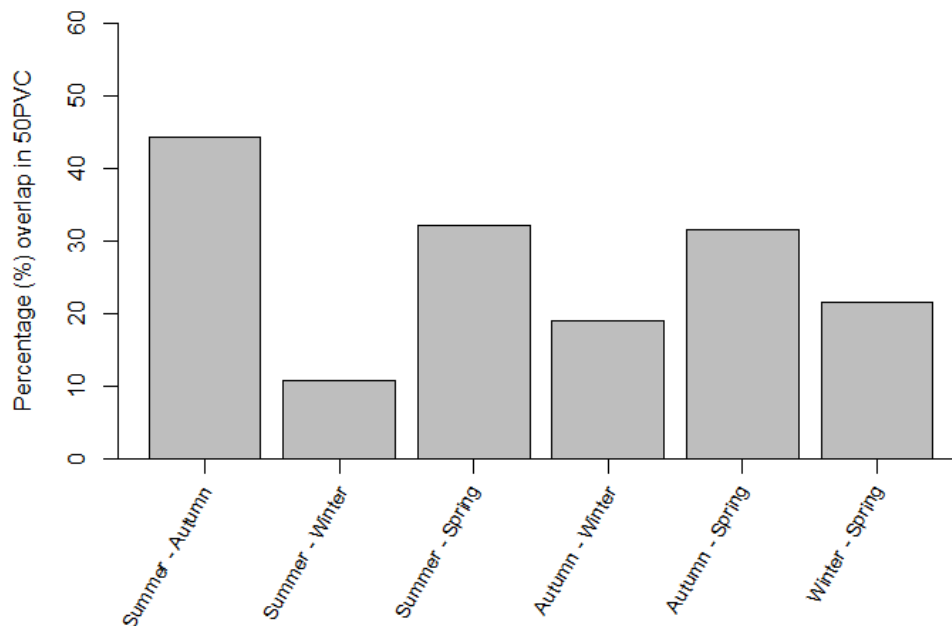


**Figure 2.4.** Seasonal kernel density estimates (h-value = 10000m, cell size = 200m<sup>2</sup>), 50 and 95 Percent Volume Contours (PVC) of bottlenose dolphin groups in Doubtful Sound between 2005 and 2018. Colours indicate relative density; hot colours are higher densities and cold colours are lower densities. Solid black line represents the limits of the 50PVC and the dotted line the limits of the 95PVC.

The total area of core bottlenose dolphin habitat was smallest (more condensed) during summer, and largest (more dispersed) during spring (Figure 2.5). Comparison among seasons, made via the percentage overlap in 50PVC area, showed that summer and winter had the least overlap at less than 15%, while summer and autumn had the highest, greater than 40% (Figure 2.6).



**Figure 2.5.** Total area of bottlenose dolphin core habitat in Doubtful Sound, represented by 50 percent volume contour (50PVC) for each season: summer, autumn, winter and spring. Produced from Kernel Density Estimation (h-value=10000m, cell size = 200m<sup>2</sup>).

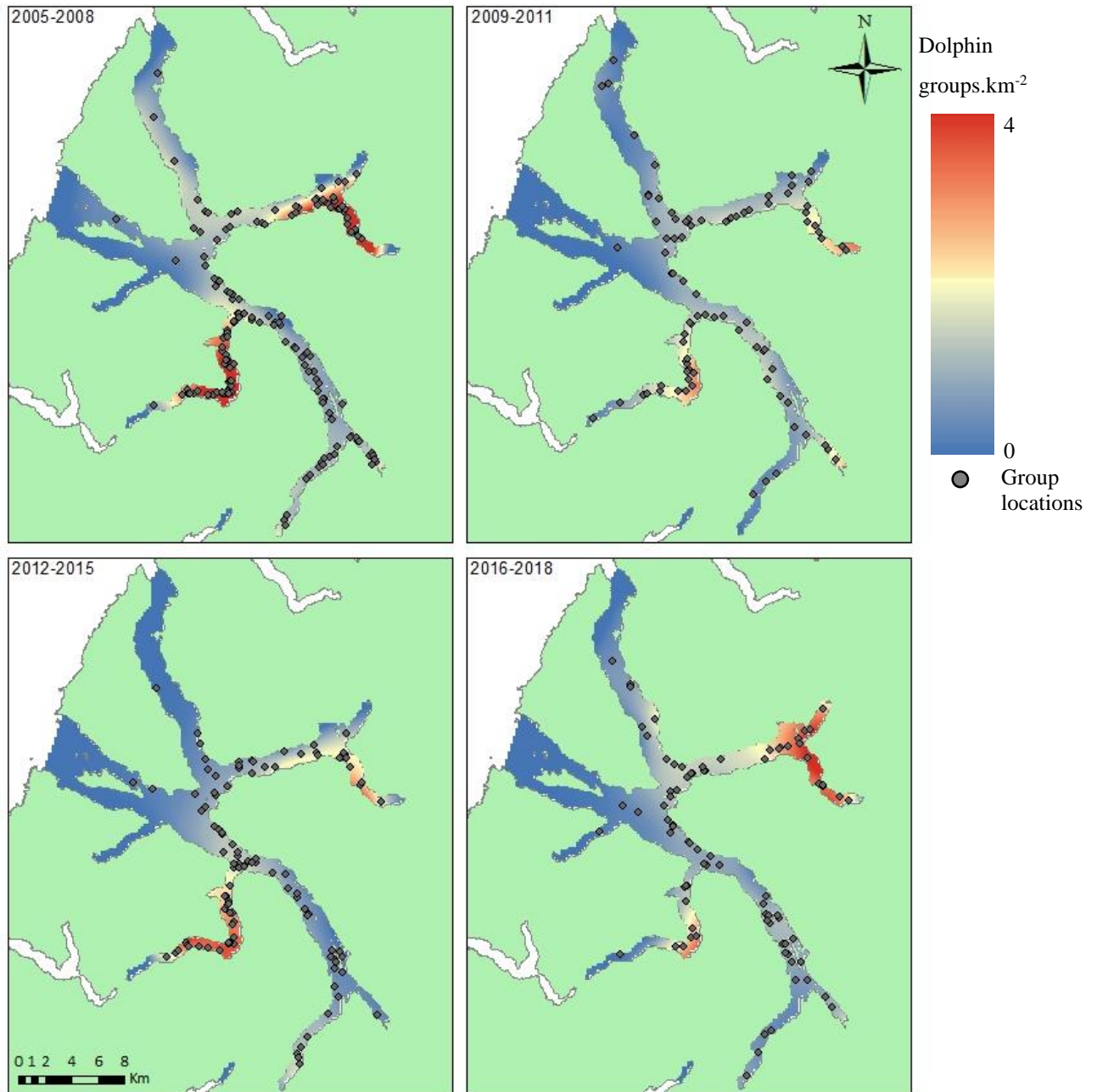


**Figure 2.6.** Percentage overlap between bottlenose dolphin core habitat in Doubtful Sound, represented by 50 percent volume contours (50PVC), from each season: summer, autumn, winter and spring. Produced from Kernel Density Estimation (h-value=10000m, cell size = 200m<sup>2</sup>).



### *Longitudinal distribution analysis*

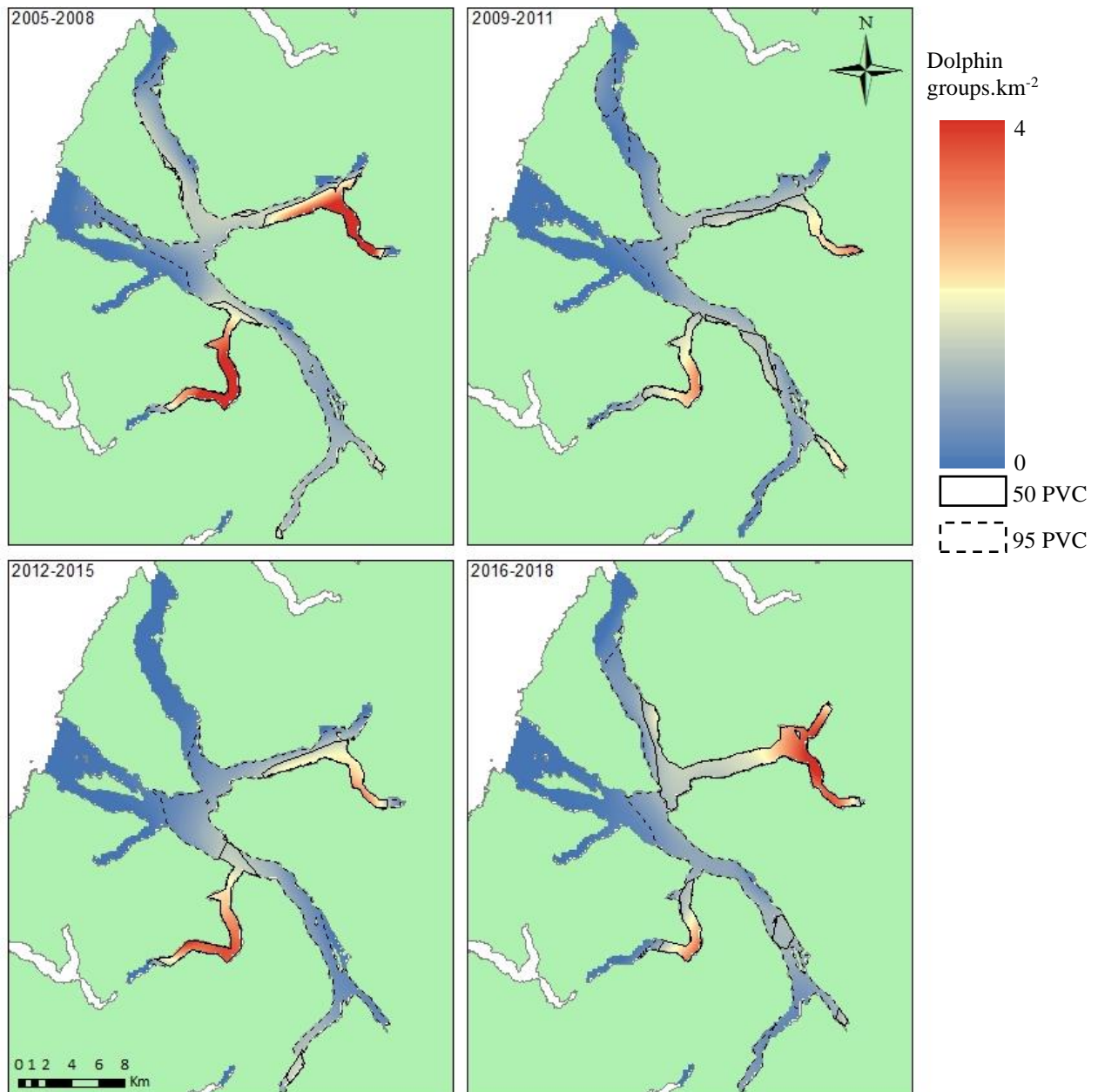
Bottlenose dolphins were consistently sighted more frequently in the inner fjord areas than the outer, regardless of the time period (Figure 2.7). Although there is some variation in the number of sightings at different locations between time periods, they were consistently clustered in Bradshaw Sound, Crooked Arm and inner Doubtful Sound. Density estimates were generally higher in areas with a higher number of sightings; an exception to this was the inner main channel in Doubtful Sound.



**Figure 2.7.** Bottlenose dolphin group locations in Doubtful Sound over different time periods: 2005-2008 (n=157), 2009-2011 (n=86), 2012-2015 (n=106) and 2016-2018 (n=83). Sightings are superimposed on seasonal kernel density estimates (h-value = 7400m, cell size = 200m<sup>2</sup>). Colours indicate relative density; hot colours are higher densities and cold colours are lower densities.

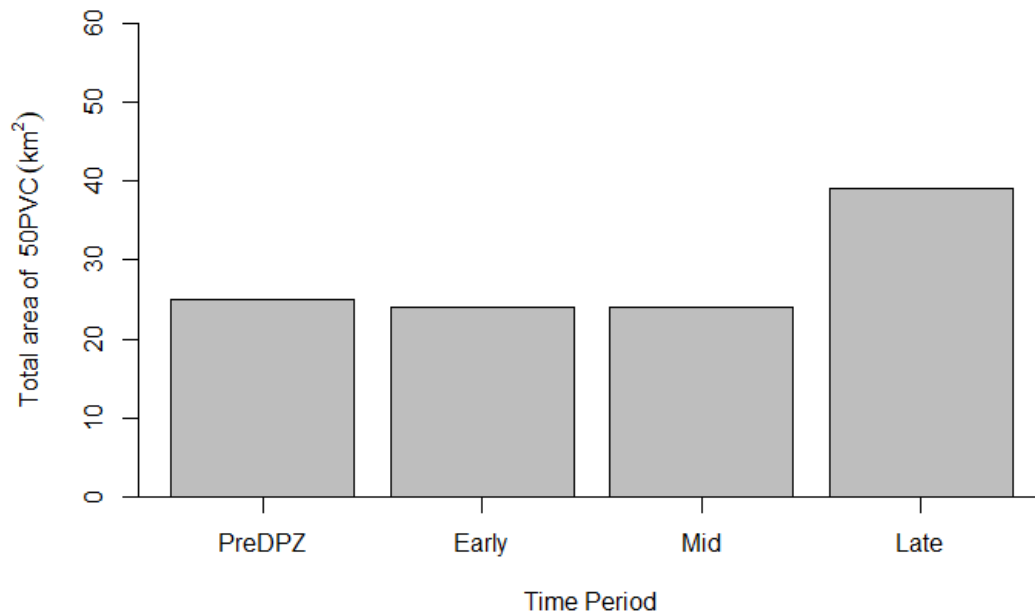


Habitat use in Doubtful Sound showed a high level of consistency over time, in both the areas where dolphins were sighted (Figure 2.7) and subsequent 50PVCs (Figure 2.8). For all time periods 50PVCs were located in Crooked Arm and the northeast end of Bradshaw Sound. For three of the time periods (2005-2008, 2009-2011 and 2016-2018) 50PVCs were also observed in the inner fjord, including Deep Cove and Hall Arm. In the latest time period the 50PVC in Bradshaw Sound extended into Thompson Sound and a smaller 50PVC in Crooked Arm was observed (Figure 2.8).

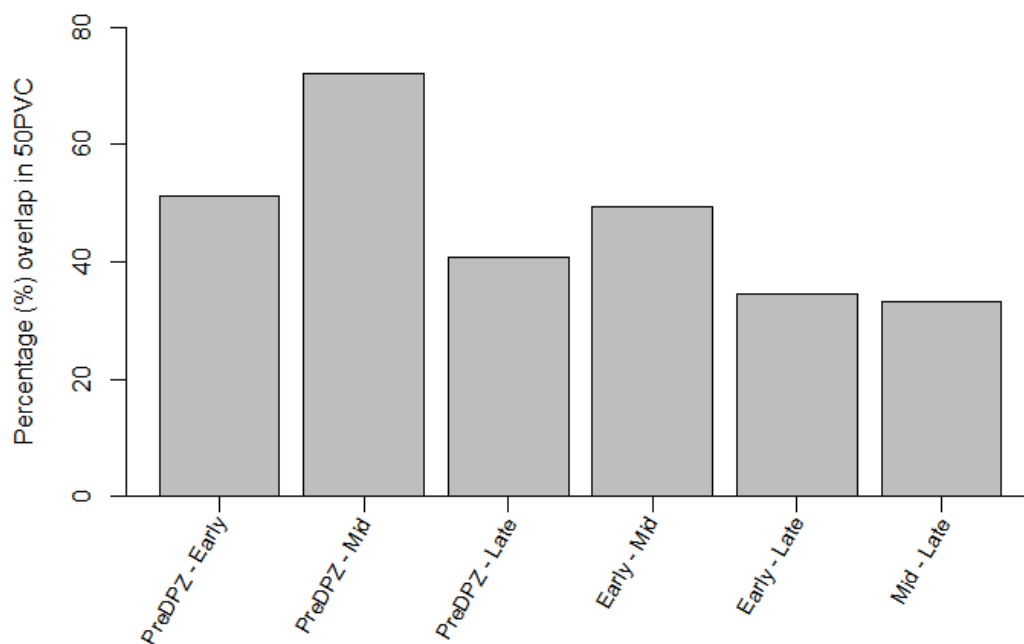


**Figure 2.8.** Longitudinal kernel density estimates ( $h$ -value = 7400m, cell size = 200m<sup>2</sup>), 50 and 95 Percent Volume Contours (PVC) of bottlenose dolphin groups in Doubtful Sound over different time periods. Colours indicate relative density; hot colours are higher densities and cold colours are lower densities. Solid black line represents the limits of the 50PVC and the dotted line the limits of the 95PVC.

The total area of bottlenose dolphin core habitat in Doubtful Sound was similar from 2005-2015, with a larger core habitat observed from 2016-2018 (Figure 2.9). Consistency in habitat use over time was supported by a comparison of the percentage area overlap between time periods, with the latest time period the most different from the others (Figure 2.10). All time periods had a 50PVC area with an overlap above 30%.



**Figure 2.9.** Total area of bottlenose dolphin core habitat in Doubtful Sound, represented by 50 percent volume contour (50PVC) in four time periods: PreDPZ (2005-2008), Early (2009-2011), Mid (2012-2015), and late (2016-2018). Produced from Kernel Density Estimation (h-value=7400m, cell size = 200m<sup>2</sup>).

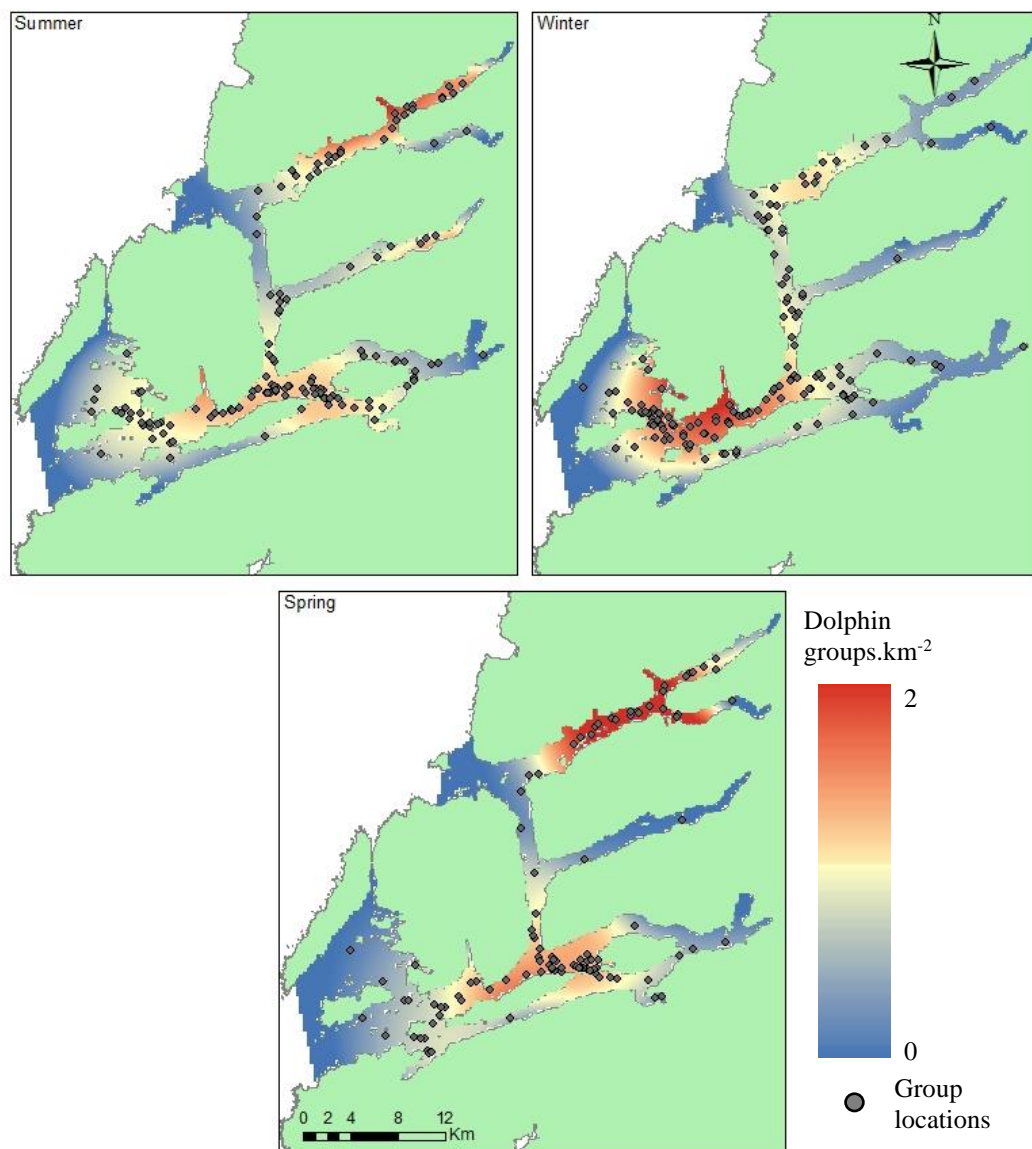


**Figure 2.10.** Percentage overlap between bottlenose dolphin core habitat in Doubtful Sound, represented by 50 percent volume contours (50PVC), from each time period: PreDPZ (2005-2008), Early (2009-2011), Mid (2012-2015) and Late (2016-2018). Produced from Kernel Density Estimation (h-value=7400m, cell size = 200m<sup>2</sup>).

### 2.3.2 Dusky Sound

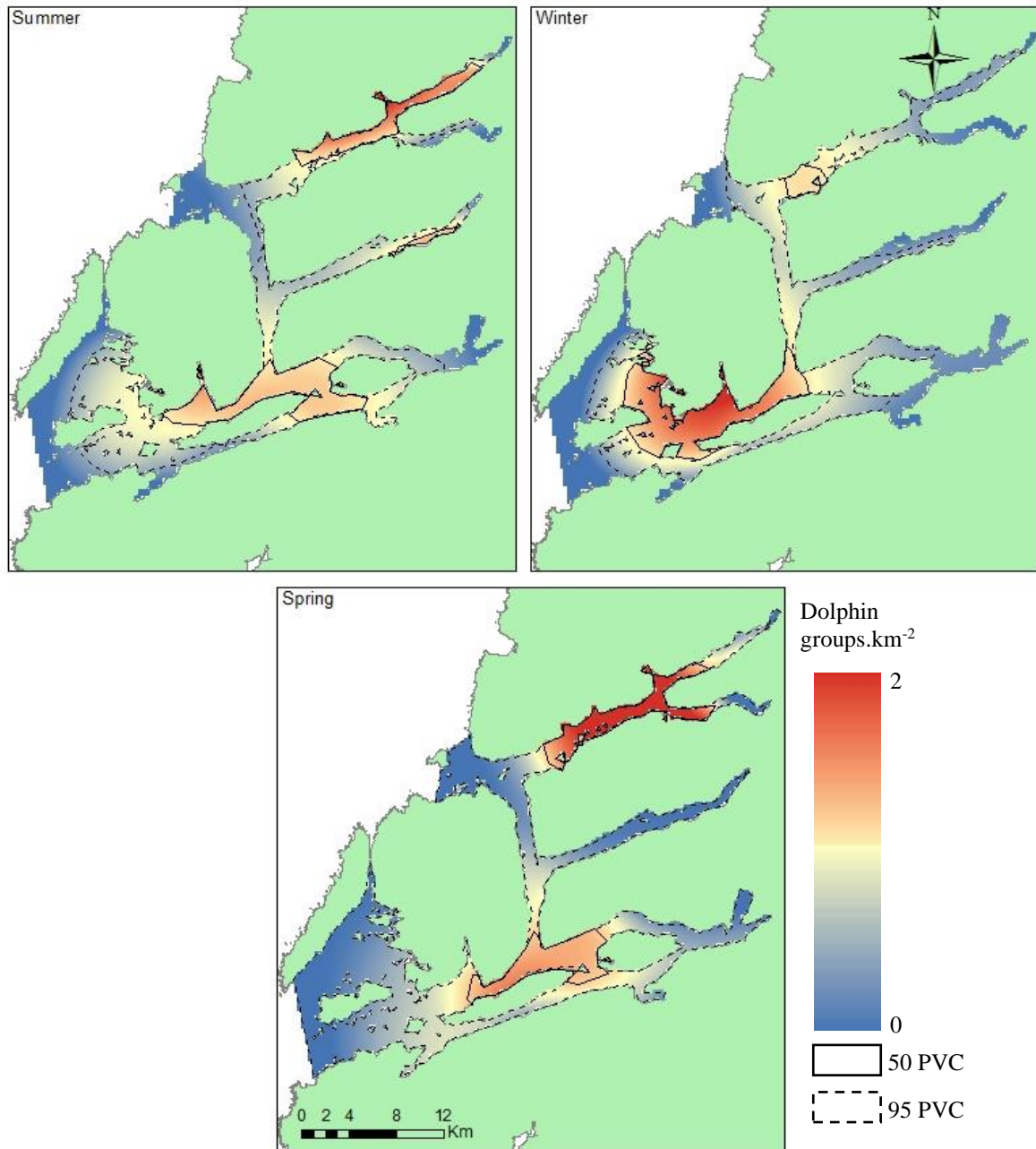
#### *Seasonal distribution analysis*

Habitat use by dolphins in Dusky Sound showed less obvious seasonal variation than in Doubtful Sound. When group sightings were partitioned by season the greatest change was observed in the inner fjord: summer had more sightings on the east side of Cooper Island, Wet Jacket and Vancouver Arm then winter (see Figure 2.2 for place names; Figure 2.11). Sightings observed during spring were most similar to those observed in summer. Density estimates throughout the fjord reflected the pattern in observed sightings, higher densities in areas with a higher intensity of sightings.



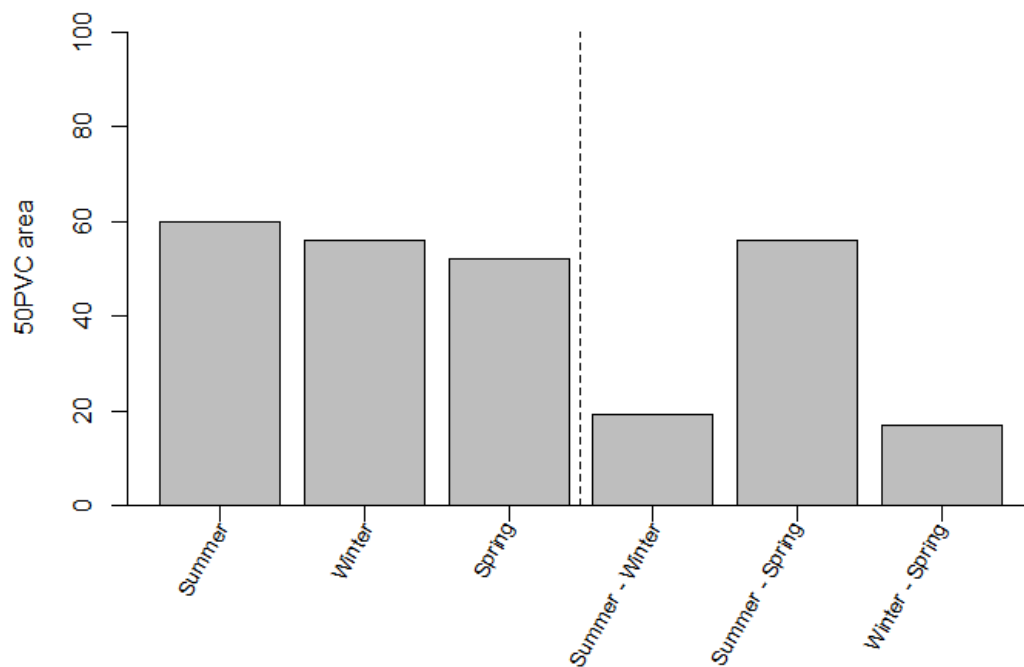
**Figure 2.11.** Seasonal bottlenose dolphin group locations in Dusky Sound between 2009 and 2018: summer (n=133 sightings), winter (n=137 sightings), and spring (n=102 sightings). Sightings are superimposed on seasonal kernel density estimates (h-value = 14100m, cell size = 300m<sup>2</sup>). Colours indicate relative density; hot colours are higher densities and cold colours are lower densities.

The KDE analysis revealed that there was consistent use of different areas in Dusky Sound among seasons. Bottlenose dolphin core habitat, as shown by 50PVC, however, had more variation, with a shift to the outer fjord during winter. For example, The Acheron Passage formed part of the core habitat in winter, and the innermost parts of the fjord were avoided (Figure 2.12).



**Figure 2.12.** Seasonal kernel density estimates ( $h$ -value = 14100m cell size =  $300\text{m}^2$ ) 50 Percent Volume Contours (PVC) and 95PVCs of bottlenose dolphin habitat use in Dusky Sound between 2009 and 2018. Colours indicate relative density; hot colours are higher densities and cold colours are lower densities. Solid black line represents the limits of the 50PVC and the dotted line the limits of the 95PVC.

The total area of bottlenose dolphin core habitat was similar between all seasons in Dusky Sound (Figure 2.13). The core habitat was most similar between summer and spring with the greatest percentage overlap (>50%). Core habitat in winter was most different with less than 20% overlap in 50PVC between either summer or spring (Figure 2.13).

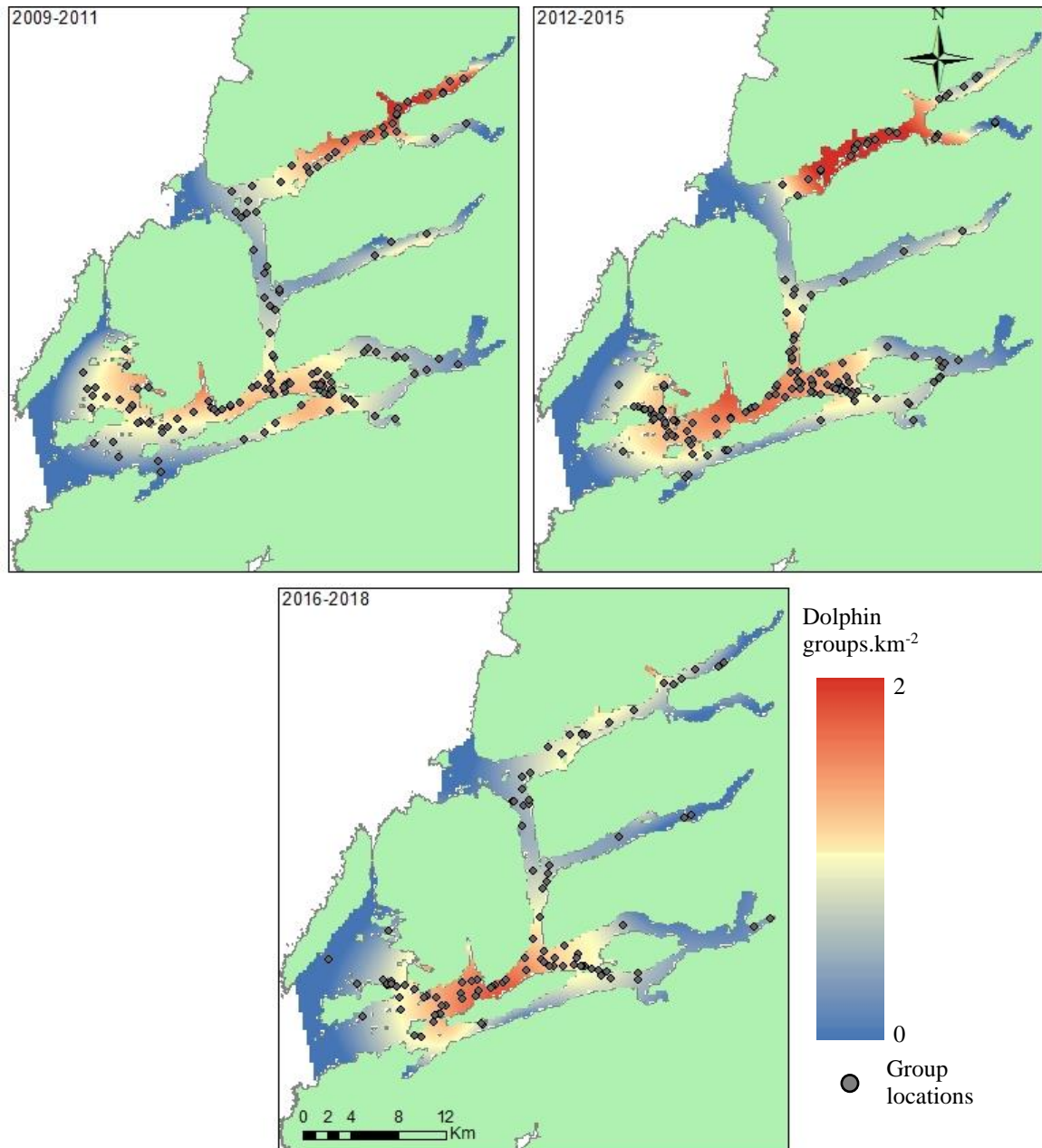


**Figure 2.13.** Total area (km<sup>2</sup>) and the area overlap of bottlenose dolphin core habitat in Dusky Sound between seasons: summer, winter and spring. Represented by 50PVC, produced from Kernel Density Estimation (h-value=14100m, cell size = 300m<sup>2</sup>).



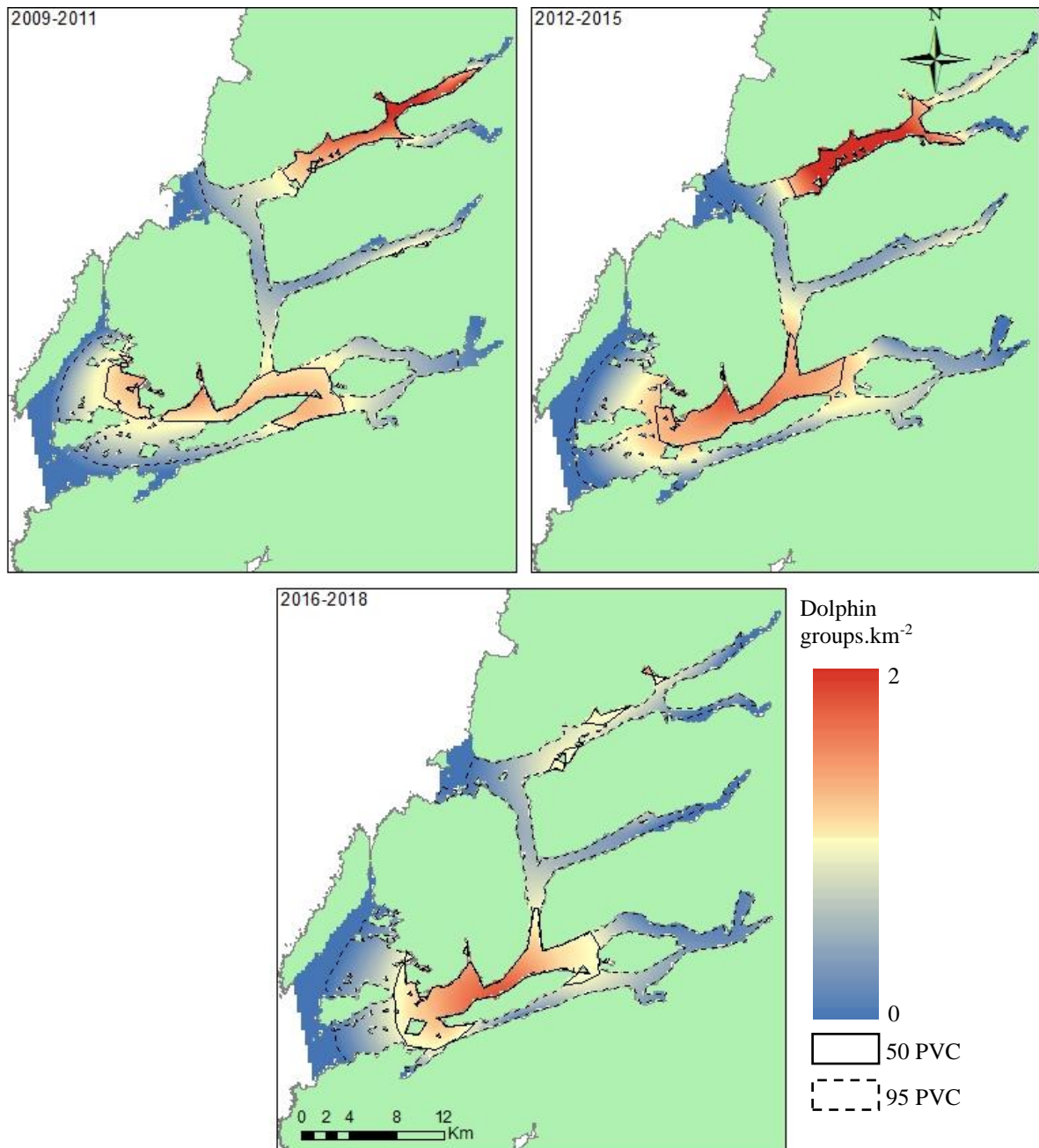
### *Longitudinal distribution analysis*

Bottlenose dolphins were sighted in all areas of Dusky Sound, except the very outer parts of the fjord (i.e. the entrance to Breaksea Sound and west of Anchor Island), a pattern that was consistent through time (Figure 2.14). Areas with a high intensity of sightings were observed in Vancouver Arm, the Bowen Channel, the south end of the Acheron Passage and east of Anchor Island. These areas consistently had high sighting intensity in each time period, and density estimates reflect this.



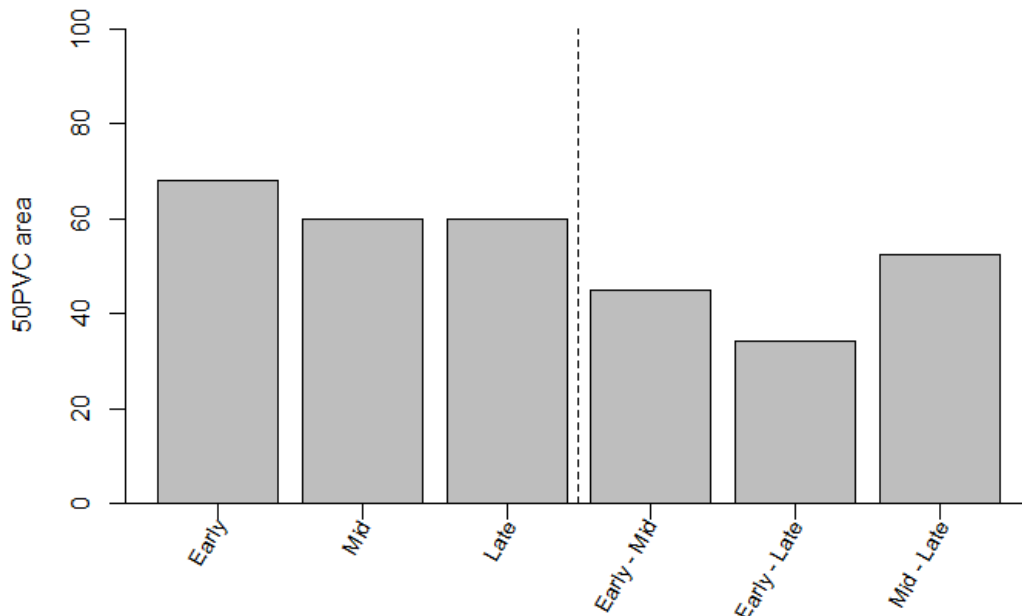
**Figure 2.14.** Bottlenose dolphin group locations in Dusky Sound at different time periods: 2009-2011 ( $n=133$ ), 2012-2015 ( $n=139$ ) and 2016-2018 ( $n=100$ ). Sightings are superimposed on temporal kernel density estimates ( $h$ -value = 12300m, cell size = 300m<sup>2</sup>). Colours indicate relative density; hot colours are higher densities and cold colours are lower densities.

Bottlenose dolphin core habitat, as shown by 50PVC, was consistent in Dusky Sound over time (Figure 2.15). Two main areas appeared to consistently have high habitat use: Breaksea Sound (from the John Islands to Vancouver Arm) and in the Bowen Channel in Dusky Sound (Figure 2.15). In the latest time period (2016-2018) habitat use around the Bowen channel was similar to the other time periods, however core habitat in Vancouver Arm and Breaksea Sound was more fragmented.



**Figure 2.15.** Longitudinal kernel density estimates (h-value = 12300m, cell size = 300m<sup>2</sup>), 50 Percent Volume Contours (PVC) and 95PVCs of bottlenose dolphin groups in Dusky Sound over different time periods. Colours indicate relative density; hot colours are higher densities and cold colours are lower densities. Solid black line represents the limits of the 50PVC and the dotted line the limits of the 95PVC.

Total area of bottlenose dolphin core habitat was similar between all time periods in Dusky Sound (Figure 2.16). Consistency in habitat use between time periods was observed with greater than 30% overlap between all seasons (Figure 2.16). The greatest difference in core habitat was observed between the early time period (2009-2011) and later time periods.

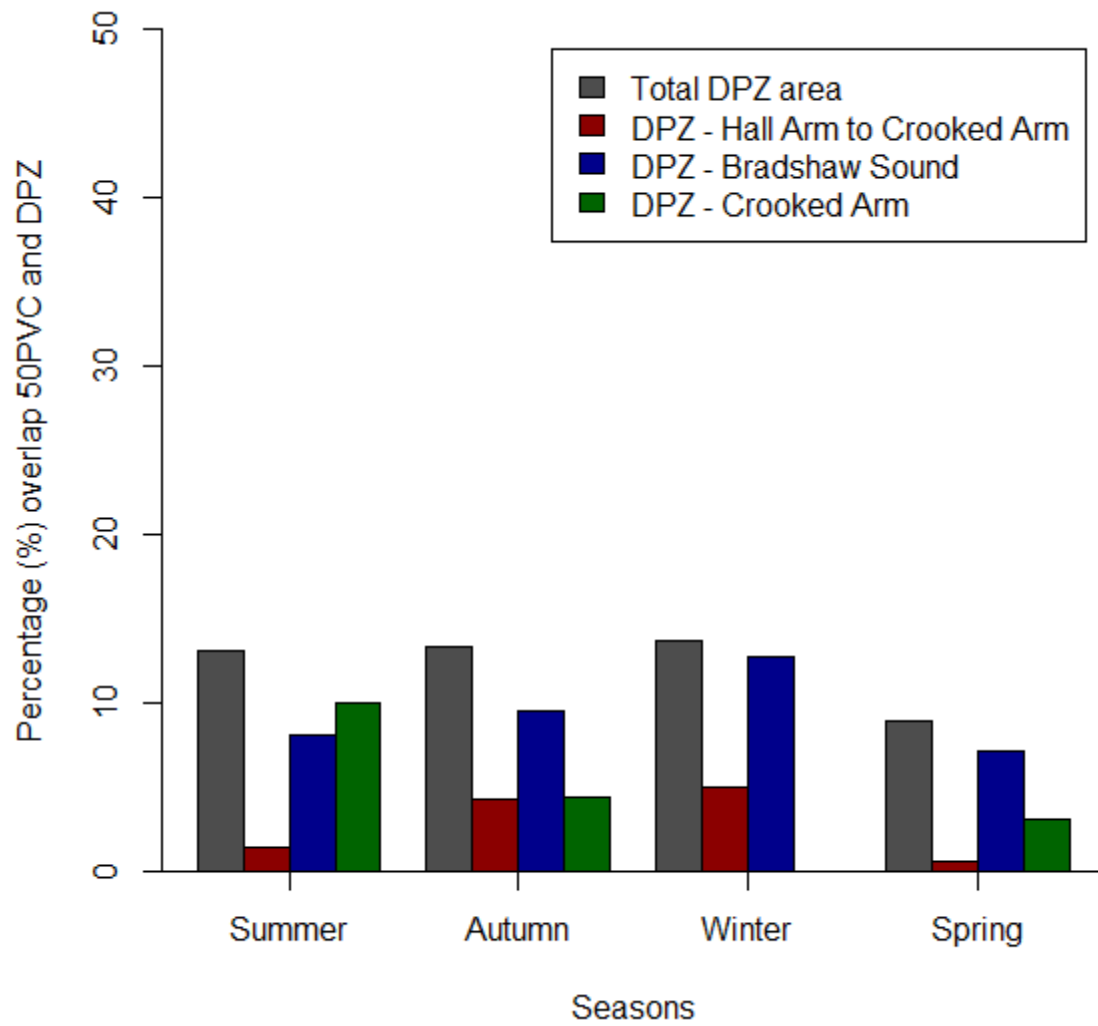


**Figure 2.16.** Total area (km<sup>2</sup>) and the area overlap of bottlenose dolphin core habitat in Dusky Sound between time periods: Early (2009-2011), Mid (2012-2015) and Late (2016-2018). Represented by 50PVC, produced from Kernel Density Estimation (h-value=12300m, cell size = 300m<sup>2</sup>).

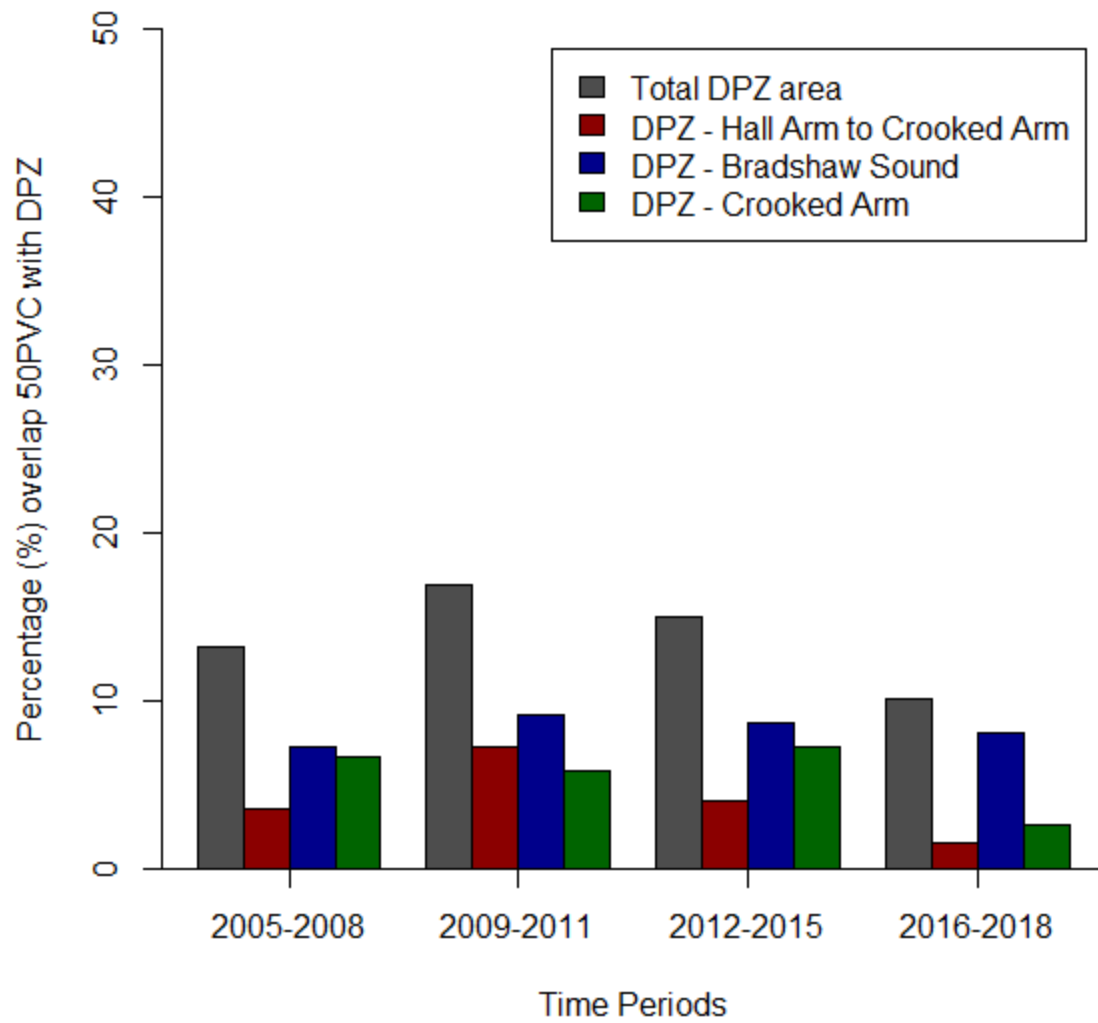
### 2.3.3 Doubtful Sound Dolphin Protection Zones

Overlap of dolphin core habitat (50PVCs), and the current spatial management in Doubtful Sound (DPZs), was evaluated seasonally and temporally (Figure 2.17, 2.18). The overlap between DPZs and core habitat was low, less than 20% for all seasons (Figure 2.17) and time periods (Figure 2.18). The DPZ extending between Hall and Crooked Arms consistently had low overlap with core areas. In summer the Crooked Arm DPZ had the highest percent overlap, while in winter no overlap was observed (Figure 2.17). The Bradshaw Sound DPZ had the most consistent observed percent overlap through time, with a slight increase during winter. In the later time period percent overlap decreased in both the Crooked Arm DPZ and the DPZ extending between Hall and Crooked Arms (Figure 2.18).





**Figure 2.17.** Comparison of the percent overlap in Doubtful Sound between the core habitat of bottlenose dolphins (represented by 50 percent volume contours, 50PVC) and each dolphin protection zone in Doubtful Sound for each season: summer, autumn, winter and spring. Core habitat of the dolphins was produced with Kernel Density Estimation (h-value=10000m, cell size = 200m<sup>2</sup>).



**Figure 2.18.** Comparison of the percent overlap in Doubtful Sound between the core habitat of bottlenose dolphins (represented by 50 percent volume contours) and each dolphin protection zone in Doubtful Sound for each time period: 2005-2008 (PreDPZ), 2009-2011 (Early), 2012-2015 (Mid) and 2016-2018 (Late). Core habitat of the dolphins was produced with Kernel Density Estimation (h-value=7400m, cell size = 200m<sup>2</sup>).

## 2.4 Discussion

Chapter two resolved the distribution of bottlenose dolphins in both Doubtful and Dusky Sounds in order to understand how they are using their habitat. Although habitat use includes aspects of both behaviour and distribution, most of what the dolphins are doing is not observable, therefore the term habitat use is used to describe these distribution patterns. Habitat use by bottlenose dolphins, in both Doubtful and Dusky Sounds, showed clear spatial and seasonal variation. Two main core areas were evident in these fjords, the end of Bradshaw Sound and Crooked Arm in Doubtful Sound, and Breaksea Sound and the Bowen channel in Dusky Sound. Seasonal variation was most obvious between summer and winter, shifts in the core areas away from the inner fjord during winter were observed in both Doubtful and Dusky Sounds. Dolphin habitat use during spring in Dusky Sound had an opposite trend to what is observed in Doubtful Sound, in that it was most condensed rather than most dispersed. In Doubtful Sound summer had the most condensed core habitat. Habitat use was consistent over long periods in both fjords, showing only subtle changes over the approximately decadal duration of this study (Doubtful 2005-2018, Dusky 2009-2018). The later time periods (2016-2018) in both fjords were the most different, becoming larger (Doubtful Sound) or slightly more fragmented (Dusky Sound) than in previous time periods.

Seasonal variation in habitat use has been described in previous studies of the bottlenose dolphins in both fjords (Schneider 1999; Henderson 2013), and has been interpreted as reflecting physiological and reproductive requirements (Schneider 1999; Haase and Schneider 2001; Henderson et al. 2014). Henderson (2013) showed a positive correlation between sighting locations and sea surface temperature (SST), with sightings being rare in SSTs below 8°C. During winter, the surface waters of the innermost parts of fjord are coldest, sometimes forming a thin layer of ice. This may explain the shifts away from the inner fjord during this season.

Bottlenose dolphins in the Moray Firth also shift their habitat use away from cold waters in winter, a phenomenon thought to be driven by energetic requirements of thinly insulated calves (Wilson et al. 1997). A similar link between habitat use and reproductive requirements has been described in several other cetaceans: e.g. southern right whale (Rayment et al. 2015); humpback whales (*Megaptera novaeangliae*; Craig and Herman 2000); and dusky dolphins (*Lagenorhynchus obscurus*; Weir et al. 2008). Due to the strong parallels between the Fiordland bottlenose dolphins and those in the Moray Firth (e.g. residing in high latitudes and seasonality

in births) the same driver is thought to be occurring here (Schneider 1999; Haase and Schneider 2001; Henderson et al. 2014).

Although it is likely that physiological drivers are extremely important for bottlenose dolphins in Fiordland, habitat use is usually the result of multiple factors. For example, the distribution of bottlenose dolphins in Shark Bay, Australia, has been shown to be a trade-off between food availability and predation risk (Heithaus and Dill 2002). Bottlenose dolphins are top predators in the fjord environment, and will both affect the other biota and respond to them. Biotic drivers can be quick to change and can show seasonal or interannual variation, therefore seasonal trends observed in the bottlenose dolphins are likely to reflect, at least in part, normal biotic rhythms of their prey species. For example, variation in fish distributions can relate to a seasonal need for spawning habitat (Afonso et al. 2009), or changes in the abiotic conditions within an area, such as an estuary (Hagan and Able 2003). Little is known about the diet of the bottlenose dolphins in Fiordland, however, stable isotope analysis indicated the majority of food is obtained from rocky reef fish from within the fjord (Lusseau and Wing 2006).

Interestingly, this study indicated that the bottlenose dolphins showed more condensed habitat use (shown through the 50PVC) during one season. In Doubtful Sound this is observed in summer and in Dusky Sound during spring. Condensing of the core habitat could be in response to biotic factors, for example higher abundance of predators, concentrated areas of prey or social interactions associated with reproduction (Wilson et al. 1997). The bottlenose dolphins of Doubtful Sound are highly social (Lusseau et al. 2003; Johnston et al. 2017), with distinct breeding and calving periods (Henderson et al. 2014). Schneider (1999) noted that the dolphins of Doubtful Sound were seen in larger and more cohesive groups during the breeding season.

Although habitat use by the bottlenose dolphins appeared to be consistent through time, slight variation in the core habitat (50PVC) was observed. In Doubtful Sound, the core habitat in Crooked Arm shrunk, with an extension into Bradshaw Sound, in the later time period. In Dusky Sound the core habitat was more fragmented, particularly in Breaksea Sound. Although this could be due to slightly lower sample sizes, or shorter research trips during the later years, it is a trend that suggests that the continued monitoring of these populations should incorporate distribution analysis. This is especially relevant for Doubtful Sound due to the DPZ spatial-based management and will be important for Dusky Sound if similar protection is established. Consistency in habitat use by bottlenose dolphins through time is an important result for management because it suggests that spatial management applied to areas of high habitat use

would likely confer long-lasting protection. More research on habitat use has occurred in Doubtful Sound and the results of this study are comparable to research completed by Schneider (1999). Together, the two studies indicate that the current core habitat within the fjord has been important since at least 1999. A similar picture is beginning to emerge in Dusky Sound. Even though there is some indication of broad-scale change in habitat use in Doubtful Sound, with the dolphins leaving the fjord with increasing frequency (Henderson et al. 2013), the areas that they use within the fjord have remained consistent.

Changes in habitat use may easily have complex causes; they could relate to the availability and quality of prey species, shifts in predator abundance (Heithaus and Dill 2002) or reflect a behavioural reaction to tourism (Lusseau 2005). In Doubtful Sound for example, Crooked Arm is heavily used by most tour companies up to Turn Point. To do so they travel directly through a large portion of the dolphins' core habitat, which has condensed in recent years. Understanding what drives habitat use is extremely important and is investigated further in chapters three and four.

I incorporated data over a longer period than had previously been investigated, including data from before DPZs were established in Doubtful Sound. Results indicate that habitat use, in particularly the core habitat, has not dramatically changed since prior to the establishment of DPZs. These results contrast with habitat use of bottlenose dolphins through time in the Bay of Islands, NZ (Hartel et al. 2015), and the Moray Firth, Scotland (Wilson et al. 2004). In these examples both populations had established protected areas and subsequently shifted their core ranges outside of this protection over a ten-year period. In the Bay of Islands this was seen as a fine-scale habitat shift, with the broad patterns remaining the same, while in Moray Firth the dolphins were thought to have expanded their range while retaining only limited overlap with the protected area. The cause of these shifts were unknown, however in the Moray Firth it is suspected that changing prey resources were a driving cause (Wilson et al. 2004). The Fiordland populations are largely resident within their respective fjords (Williams et al. 1993; Schneider 1999; Currey et al. 2008; Henderson et al. 2013). This could imply that the environment, or the drivers of habitat use have remained reasonably consistent through time.

In this study, and in that by Henderson (2013), KDE has been an important tool to quantify the habitat use of bottlenose dolphins in Doubtful and Dusky Sounds. Improvements in the technique since Henderson's analysis meant that I could incorporate barriers to movement (land) and hence use a larger smoothing parameter. Smaller smoothing parameters resulted in

a fragmented 95PVC (Henderson 2013) potentially underestimating the importance of some areas. Having a non-fragmented 95PVC allows movement corridors to be represented. As these KDEs describe habitat use by the population it is more representative to have a range that is connected, as individuals within the population need to use the area between sightings for travel. This is the first study to attempt KDEs for bottlenose dolphins in Fiordland that accounted for the structure of the coastline. The resulting density estimates should therefore be representative of the real habitat use by dolphins in these complex habitats. One caveat should be mentioned; the smoothing parameter had to be reasonably large in order to limit apparent fragmentation of core habitat. This may result in over-smoothing, especially when a higher smoothing parameter was used for comparison between time-periods and seasons, and the edges of the 50PVC may not be perfectly reliable. This may be particularly true where estimates extend to the middle of the fjord. However, the density estimates directly reflect the sighting data, so the real effect of my choice of smoothing parameter is probably small. It would, however, be good practise to combine results from multiple distribution analyses before using these results to define appropriate spatial management.

This study is the first to look at long term habitat use of the bottlenose dolphins in both Doubtful and Dusky Sounds. It has revealed a high level of consistency over a decadal time scale. Seasonal variation reflects previous studies on habitat use. We can use the information presented in this study to help design future management, which will be discussed at the end of this thesis.

## Chapter 3

### Quantifying habitat use of bottlenose dolphins in Fiordland through generalised additive models

#### 3.1 Introduction

Understanding why a species or population uses specific habitat presents a different challenge to describing where a species is distributed. This is because determining *why* particular habitat is used requires a broad understanding of what it offers, and how that relates to the behaviour and lifecycle of the organism under study. This question is important because it can aid management decisions about how to protect the species; for example, high-use areas within a species' range can be identified, and if a formal habitat model is developed, it can be applied to areas not yet studied (Bailey and Thompson 2009; Mannocci et al. 2015). Such a model might be used to predict how distributions might shift under scenarios of environmental change, and hence guide management decisions (Torres et al. 2013). For recovering populations, understanding of habitat preferences can indicate which areas the population might recover to, and help define what might have been the historical range (Cianfrani et al. 2010; Hebblewhite et al. 2011; Torres et al. 2013).

One common method for describing drivers of distribution is the comparison of habitat characteristics with species occurrence data, typically termed Species Distribution Modelling. Species Distribution Models (SDMs) can be used to create a better understanding of how and why an animal uses an area, but also to predict distribution patterns (Rodríguez et al. 2007). There are a range of methods available, with modelling approaches becoming commonly used in ecology and for management purposes (e.g. Guisan and Thuiller 2005; Klar et al. 2008; Marubini et al. 2009; Viddi et al. 2010; Azzellino et al. 2012; Torres et al. 2013; Rayment et al. 2015). SDMs can be relatively simple, such as overlaying sightings on maps of habitat variables, and investigating correlations between single predictor variables and species occurrence. In this approach one variable is assessed at a time. More complex approaches include relating several predictor variables to the response using regression models. A variety of regression models are commonly used, from linear regression which describes simple, direct relationships between the response and predictors, to more flexible approaches such as generalized models which can deal with non-linear relationships. The latter types of relationships are, of course, more common in ecological data (Torres et al. 2008; Rayment et al. 2015).

Generalised Additive Models (GAMs) are one such approach. (Hastie and Tibshirani 1990). They are non-parametric, flexible and data-driven and can deal with non-linear responses. Because these models are additive they describe the effects of each predictor on the response while accounting for effects from other predictors present in the model (Hastie and Tibshirani 1990). This is ideal in ecological relationships because responses are usually driven by a combination of several factors. GAMs are often used for studies of cetacean habitat use, for example with bottlenose dolphins (*Tursiops truncatus*, Torres et al. 2008), common dolphins (*Delphinus sp.*; Stockin et al. 2008b), short-finned pilot whales (*Globicephala macrorhynchus*) and Blainville's beaked whales (*Mesoplodon densirostris*; Abecassis et al. 2015), fin whales (*Balaenoptera physalus*) and striped dolphins (*Stenella coeruleoalba*; Panigada et al. 2008), and southern right whales (*Eubalaena australis*; Rayment et al. 2015).

Simple SDMs have been created for the bottlenose dolphin populations in Doubtful and Dusky Sounds (Henderson 2013). In Doubtful Sound, bottlenose dolphin distribution was significantly correlated with sea surface temperature (SST), distance to the fjord entrance and distance to the fjord wall. In Dusky Sound, the predictor variables SST and distance to the fjord entrance were significantly correlated with bottlenose dolphin distribution, though the relationship was not as strong as for Doubtful Sound. Henderson (2013) used correlations and partial Mantel tests to assess the importance of each predictor over a three year time period, 2009-2012. More complex SDMs, in which the contribution of several variables can be assessed simultaneously within the same model, make more sense in this context. Habitat variables are often abiotic predictors, even though the distribution of a species will be influenced by biotic variables. This is because abiotic variables are often easier to collect, can directly influence distributions, and/or provide good proxies for biotic relationships (Martin 2001). The results in chapter two showed that habitat use through time has remained relatively consistent, therefore it is appropriate to combine data collected over a longer time, where those data are available.

The aim of this chapter is to quantitatively assess habitat use by the bottlenose dolphin populations of Doubtful and Dusky Sounds from 2005 to 2018 and 2009 to 2018, respectively. Habitat use was modelled using logistic Generalised Additive Models (GAMs), with a binary response variable, and a suite of abiotic environmental predictor variables. I aimed to find the best model (as assessed via AIC) and hence assess the relative importance of distance from the fjord entrance, distance from the fjord wall, depth, seabed slope, seabed aspect, and temperature on habitat use in Doubtful and Dusky Sounds.



## 3.2 Methods

### 3.2.1 General field methods

Locations of bottlenose dolphin groups obtained between 2005-2018 and 2009-2018 from Doubtful and Dusky Sound, respectively, were used to investigate the drivers of habitat use. Field methods, and the way in which group locations were calculated, were as described in chapter two.

### 3.2.2 Species Distribution Modelling

#### *Response Variables:*

SDMs require a response variable which accurately represents the species' distribution and a suite of environmental predictor variables which may influence this distribution. An objective approach is to use point location data, complementing “presence” points (sighting locations) with “absence” points where the species was not sighted (Pearce and Boyce 2006). Presence-absence models allow highly-used and less-used habitat to be contrasted, and can perform better than presence-only methods (Torres et al. 2008; Praca et al. 2009).

In the case of this study, presence points were locations of dolphin groups observed while surveying the fjords. Subsequent sightings of the same group can occur within the same day, but are likely to be spatially autocorrelated, i.e. dependent on where the group was previously (Swihart and Slade 1985). I attempted to minimise this spatial autocorrelation by only including the first sighting of a group, if I made multiple sightings of the same group on the same day. Within both Doubtful and Dusky Sounds the dolphins are able to access the entire fiord within 24 hours as explained in chapter two. Therefore, subsequent sightings of the same group on different days were used.

Obtaining absence locations is more complex; as absence data are generated continuously while surveying, continuous data must be converted into point locations (Torres et al. 2008). Furthermore, there is a chance that while surveying the available habitat, dolphins may be present but not sighted, or they may be absent one day and present the next. Therefore, absence data are pseudo-absence locations, which are often used when studying highly mobile species (e.g., Torres et al. 2008; Rayment et al. 2015). I obtained pseudo-absence locations from the GPS track of survey routes. Each track was uploaded to ArcMap (version 10.6.1; Environmental Systems Research Institute, Redlands, California, USA) and a 200m buffer was generated around the track using the “Buffer” tool. The 200m buffer is considered a

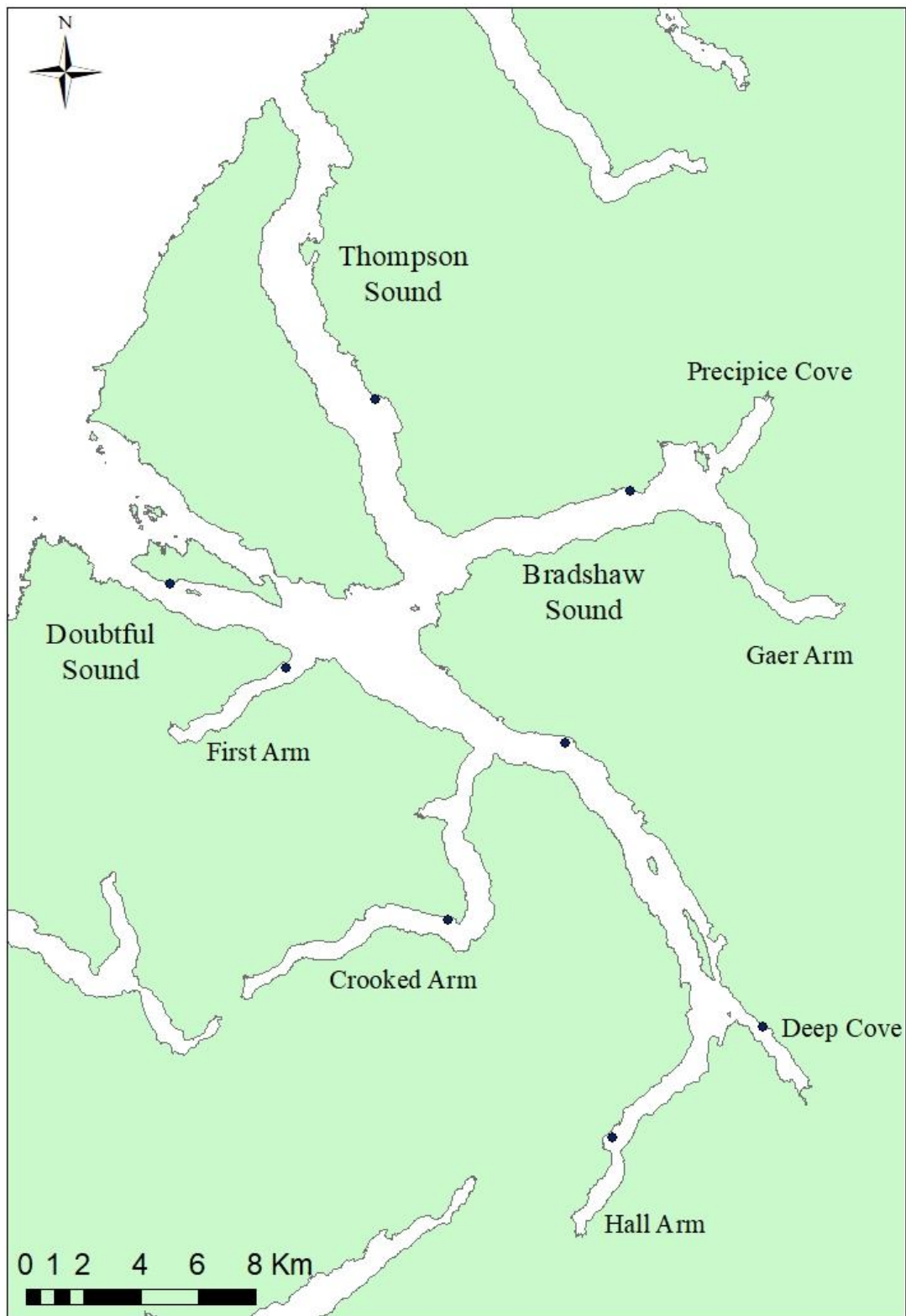
conservative estimate of the distance on either side of the research vessel (RV) that researchers would have spotted dolphins if they had been present. This buffer distance is based on combined visual/acoustic surveys used in previous research on the dolphins of Doubtful Sound (Guerra et al. 2014). Parts of the buffer were removed when they occurred concurrently to when the RV was with dolphins, as well as 15 minutes prior to and post encounter. In the remaining buffer area, an equal amount of pseudo-absence points to presence points were randomly generated using the “Generate Random Points” tool. This was repeated for every survey. Pseudo-absences were generated randomly based on the condition they were not within 200m of each other on the same day. All pseudo-absences were assigned a corresponding time, date and season based on the survey they were generated from. Some studies use a higher proportion of pseudo-absence to presence locations, because it can increase contrast and, when weighted appropriately, improve model performance (Barbet-Massin et al. 2012). When attempting to use a higher proportion of absences to presence locations, the models did not meet residual assumptions therefore, I used an equal ratio of pseudo-absence to presence locations.

#### *Predictor Variables:*

Predictor variables used to describe habitat use of bottlenose dolphins in Doubtful Sound in this study included sea surface temperature (SST), temperature at depth (19m, Henderson 2013; Abecassis et al. 2015), water depth (Stockin et al. 2008b; Viddi et al. 2010), distance to the fjord wall (Henderson 2013), distance to the fjord entrance (Henderson 2013), seabed aspect (Rogers and Leathwick 1997; Pirotta et al. 2011) and seabed slope (Azzellino et al. 2008). Predictor variables used for the population in Dusky Sound were the same, except for temperature, as those data were not available. Due to the lack of a temperature predictor in Dusky Sound, I included season as a supplementary predictor variable. All variables included in this study are considered potentially important for describing habitat use of the dolphins in the fjord environment.

Temperature is thought to be one of the most important drivers of bottlenose dolphin habitat use in Fiordland because the dolphins are living close to the southern limit of their range (Schneider 1999; Henderson 2013). I used temperature measurements at the sea surface (0.5m) and depth (19m) because one may be more relevant to explaining dolphin distribution than the other. Temperature varies both temporally and spatially throughout the fjord (Appendix 3).

SST is influenced by freshwater input, both natural (i.e. rain and runoff) and anthropogenic (the Lake Manapouri hydroelectric power station; Stanton and Pickard 1981). Temperature data have been continuously collected by Meridian Energy since 2005, using eight oceanographic monitoring buoys moored in Doubtful Sound (Figure 3.1). Each presence and pseudo-absence point was assigned SST and temperature at 19m depth, corresponding with the temperature at the closest mooring at the closest time.



**Figure 3.1.** Locations of oceanographic monitoring buoys around Doubtful Sound represented by black dots.

Depth is thought to be an important predictor variable for cetacean habitat use as it can help to describe foraging (Cañadas et al. 2002), exposure to predators (Heithaus and Dill 2006) and

potential resting habitat (Thorne et al. 2012). Data for depth were obtained from the Olex system ([www.olex.no](http://www.olex.no)) onboard the Department of Conservation's research vessel, *Southern Winds*. This system uses single-beam echo-sounder data to add detail to a bathymetric chart (Ryan et al. 2016). *Southern Wind's* Olex system compiles depth data from a range of vessels travelling throughout Fiordland, resulting in a large number of data points available for describing depth. While not as high resolution as multibeam data, Olex datasets can be a very useful source of reliable, high-resolution bathymetry (Elvenes et al. 2014). I uploaded the XYZ (Longitude/Latitude/Depth) data to ArcMap v.10.6.1., then created a Digital Elevation Model (DEM) for Doubtful and Dusky Sounds by interpolating depth from these point locations. The "IDW" tool was used with a final cell resolution of 50m<sup>2</sup> (Curtarelli et al. 2015). This method weighs point values based on distance from the cell, with 12 depth points being used for each cell. Points close to the cell were given a power of two, making them more influential to the final depth. Although these data do not account for tide, the tidal range in this area is small (<2m), and the dataset has a high sampling intensity throughout both Doubtful and Dusky Sounds.

Distance to the fjord entrance has previously been described as an important predictor of habitat use for bottlenose dolphins in Fiordland (Schneider 1999; Henderson 2013). It can help to describe environmental gradients within the fjord, as well as the possible influence that oceanic water might have on distribution. To calculate the distance of each response variable to the fjord entrance, I used the "Cost path" tool in ArcMap. This tool uses cells assigned with a potential cost to determine a realistic pathway the dolphins might use to avoid the path crossing land. A cost raster (cell size=100m<sup>2</sup>) was created which assigned a cost of 0.1 to water cells and one to land cells. The "least cost" path was calculated from each presence and pseudo-absence point to a line drawn across the entrance of the fjords.

In Doubtful Sound, the dolphins show a close association with the fjord wall (Henderson 2013). For this reason, distance to wall was included as a predictor variable for both Doubtful and Dusky Sound. To calculate the distance from each presence and pseudo-absence point to the wall the "Near" tool was used in ArcMap v10.6.1.

Seabed slope is an important environmental descriptor in Fiordland, due to the u-shaped fjord systems creating steep fjord walls. In other studies it has been used to describe topography and foraging areas for cetaceans (e.g. Azzellino et al. 2008). A slope raster was generated by applying ArcMap's "slope" tool to the previously calculated depth raster.

Aspect has been used as a proxy for solar radiation in ecological modelling (Tian et al. 2001; Bennie et al. 2008), and is incorporated as a predictor here. In Fiordland, walls with a more northern aspect likely receive more sunlight than those with a southerly aspect (Cornelisen et al. 2007). Thus aspect may help to describe potential biotic variation within the study site. To calculate the aspect of the fjord walls the “Aspect” tool was used in ArcMap v.10.6.1. Values of depth, slope and aspect were obtained for each presence and pseudo-absence point by applying the “extract multi-values to points” tool to the respective raster.

### *Generalised Additive Models*

I produced GAMs with a logit-link function using the “mgcv” package (Wood 2017) in the R environment (R Development Core Team 2018). GAMs were built using the binomial presence/absence dolphin occurrence data as a response variable and all combinations of available predictor variables. The global models were therefore: presence/absence ~ SST + Temperature at 19m + distance to the fjord wall + distance to the fjord entrance + Depth + Slope + Aspect in Doubtful Sound and presence/absence ~ distance to the fjord wall + distance to the fjord entrance + Depth + Slope + Aspect in Dusky Sound. Over-fitting the models is a potential risk, which can be mitigated by limiting the degrees of freedom for continuous predictor variables. I used thin-plate regression splines to smooth continuous predictor variables and a cubic-cyclic spline for “Aspect”, and limited the degrees of freedom (k) to a maximum of five (e.g. Rayment et al. 2015). Interactions between predictors can make the model less efficient and there can be difficulties in interpreting the results. To aid in interpretation I did not include interaction terms (Yee and Mitchell 1991). GAMs cannot handle missing variables (Wood 2017), therefore only response variables with a complete set of predictor variables were used in the final analysis.

### *Model Selection*

Models were tested for concurvity, a similar measure to collinearity that describes non-linear dependencies in the predictor variables (Ramsay et al. 2003; Amodio et al. 2014). If estimated pairwise concurvity of predictors was above 0.3 (He et al. 2006) it was decided that these predictor variables were correlated and could not be included in the same model. To determine the best predictor to use, univariate models were made of the correlated predictor variables and model performance was tested. The predictor variable with the lowest deviance explained in a

univariate model was removed, and the model refitted without this predictor. This process was repeated until the model had only non-correlated predictor variables.

After determining the final full model, I used backwards stepwise model selection to rank potential models. This method determines the top model by removing the predictor with the highest p-value and ranking this new model using Akaike's Information Criterion (AIC; Akaike 1973) using the package "MuMIn" in the R environment (Barton 2018). AIC ranks models by fit while penalising model complexity. This process was repeated using the new model as a template until the model with the lowest AIC value was found. Model ranks were checked using the dredge function in the "MuMIn" package. Including information from models with similar performance or those that are closely ranked (i.e. within two AIC points) to the top model is considered good practice (Burnham et al. 2011). This is because the top model is based on an estimate, with additional information often contained within closely ranked models. Therefore, I presented results from all models within two AIC points to the model, so that important relationships were not ignored.

The index of relative importance (IRI) was calculated for predictors included in the top model and those in models within two AIC points. The IRI takes into account the weights of all models the predictor occurs in and the frequency of occurrence of that predictor. I calculated IRI for each predictor in the top model and those within two AIC points using model averaging with the "MuMIn" package in R. This enables a comparison of the predictors used, so that a predictor variable included in only one model with a high p-value can be considered less influential on bottlenose dolphin distribution than one included in all closely ranked models.

### *Residual checking*

Residual checks are important to ensure that the data meet model assumptions. The key model assumptions are independence of datapoints and constant variance of scaled residuals. Within the package "mgcv" gam.check can be used to diagnose model residuals as well as the effect of limiting the degrees of freedom on smoothing of predictor variables. Diagnostic plots for binary data, however, are difficult to interpret (Landwehr et al. 1984; Zuur et al. 2009). Therefore residual checks for the best model were completed using a simulation-based approach from the "DHARMA" package (Hartig 2019). This package uses the "simulateResiduals" function to create scaled residuals from the fitted model. To do this, a new dataset is simulated, calculating the cumulative distribution of simulated values for each

observed value and generating a corresponding quantile value (Hartig 2019). This would mean that a scaled residual value of 0.5 would correspond to having half the observed values higher and half lower. Scaled residuals were standardised between zero and one, resulting in easily interpretable diagnostic plots (Hartig 2019). When the scaled residuals are plotted against observed residuals, comparing deviations from the expected distribution to deviations in the observed distribution, they should fall along the one-one line in the resulting qq-plot. Departure from the line indicates that the model departs from model assumptions. Models produced for Doubtful Sound met model assumptions (see Appendix 4). For models in Dusky Sound, when scaled residuals were plotted against the observed residuals there was little deviation from the one-one line observed (Appendix 5). The Kolmogorov-Smirnov test, a nonparametric test of the equality of continuance, however, was slightly significant ( $p\text{-value} = 0.04$ ) which indicates there may be a marginal lack of fit.

#### *Spatial autocorrelation*

Spatial autocorrelation is a measure of similarity between datapoints as a function of the spatial distance separating each measurement (Bjørnstad and Falck 2001). Because where animals go next is dependent on where they were last, autocorrelation among location points is inevitable. To reduce spatial and temporal autocorrelation I used only one location of a group per day. Because bottlenose dolphins in Doubtful and Dusky Sounds can cover their entire within-fiord habitat within 24 hours, sightings on subsequent days should be independent (see Ch. 2). The degree of spatial autocorrelation can also be tested statistically; I used correlograms of the residuals to test the degree of spatial autocorrelation for the top ranked models (Bjørnstad and Falck 2001; Zuur et al. 2009). Correlograms were produced using the package “ncf” in R and indicated that spatial autocorrelation was not an issue in my models (Appendix 6; 7).



### 3.3 Results

After data with missing values were removed, there were 402 and 374 presence locations available for use in the Species Distribution Models for Doubtful Sound and Dusky Sound, respectively. Pairwise concavity estimates from habitat models in Doubtful Sound indicated that depth was correlated with distance from the wall and slope (concurvity > 0.3; Table 3.1). For SDMs in Dusky Sound, pairwise concavity estimates indicated again that distance from the wall and depth were correlated (Table 3.2). As univariate models of depth explained less deviance than distance from the wall, depth was removed from further models (Appendix 8).

**Table 3.1.** Estimated pairwise concavity for smoothed (represented by s) terms of predictor variables for bottlenose dolphins in Doubtful Sound: distance from the entrance (s(Dist\_Ent\_km)); distance from the fjord wall (s(Dist\_Wall\_m)); depth (s(Depth)); slope (s(Slope)); aspect (s(Aspect)); sea surface temperature at 0.5m depth (s(SST0.5)); and temperature at 19m depth (s(Temp19)). Estimates highlighted in bold indicate that concavity between the corresponding predictors was greater than 0.3, above this, predictors are considered highly correlated.

	s(Dist_Ent_km)	s(Dist_wall_m)	s(Depth)	s(Slope)	s(Aspect)	s(SST0.5)	s(Temp19)
s(Dist_Ent_km)	1.000	0.107	0.252	0.118	0.025	0.031	0.008
s(Dist_wall_m)	0.098	1.000	<b>0.435</b>	0.020	0.027	0.004	0.005
s(Depth)	0.164	<b>0.341</b>	1.000	0.077	0.008	0.010	0.003
s(Slope)	0.110	0.029	0.045	1.000	0.014	0.016	0.006
s(Aspect)	0.026	0.022	0.018	0.012	1.000	0.002	0.002
s(SST0.5)	0.039	0.009	0.014	0.010	0.010	1.000	0.285
s(Temp19)	0.027	0.004	0.011	0.013	0.002	0.280	1.000

**Table 3.2.** Estimated pairwise concavity for smoothed terms of predictor variables of bottlenose dolphin presence in Dusky Sound: distance from the entrance (s(Dist\_Ent\_km)); distance from the fjord wall (s(Dist\_Wall\_m)); depth (s(Depth)); slope (s(Slope)); aspect (s(Aspect)). Estimates highlighted in bold indicate that concavity between the corresponding predictors was greater than 0.3, above this, predictors are considered highly correlated.

	s(Dist_Ent_km)	s(Dist_wall_m)	s(Depth)	s(Slope)	s(Aspect)
s(Dist_Ent_km)	1.000	0.010	0.014	0.034	0.008
s(Dist_wall_m)	0.007	1.000	<b>0.315</b>	0.033	0.012
s(Depth)	0.019	0.232	1.000	0.058	0.012
s(Slope)	0.011	0.034	0.037	1.000	0.013
s(Aspect)	0.005	0.009	0.003	0.008	1.000

### 3.3.1 Model Selection and Results - Doubtful Sound

The top ranked model in Doubtful Sound included distance to the entrance, distance to the wall and slope as important predictor variables (Table 3.3). The next two models were within two AIC points of the top model, and included the same three predictors, as well as one of either temperature at 19m depth or SST. The percentage deviance explained was similar amongst all of the top three models, and in all cases was below 10%. All predictors included in the top model had statistical significance in explaining distribution, were equally important and included in all models within two AIC ( $\chi^2$  p-value < 0.05, IRI = 1; Table 3.4). Additional predictors included in lower ranked models (within two AIC points) were not statistically significant (Table 3.4).

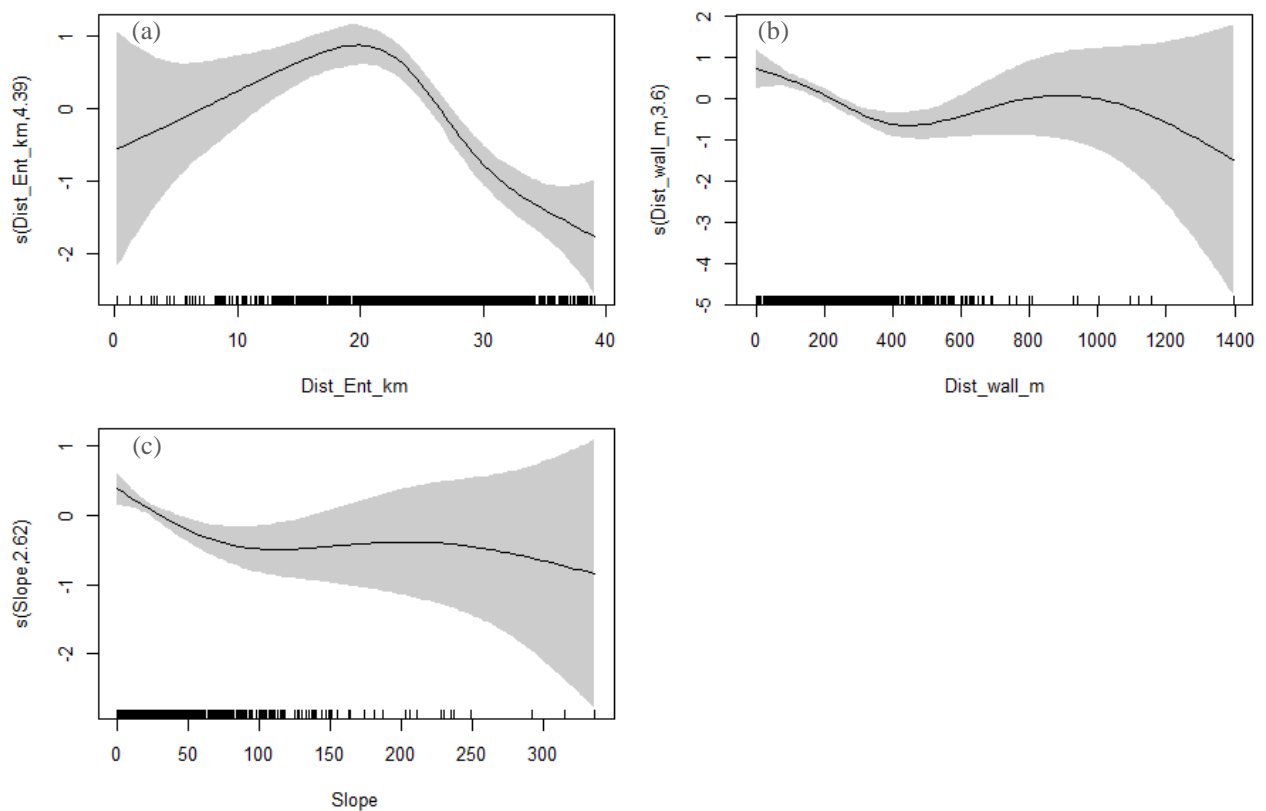
**Table 3.3.** Statistics and ranks of logistic regression models on presence of bottlenose dolphins in Doubtful Sound. Models are ranked by Akaike Information Criterion (AIC). Included are the predictors, distance to the fjord entrance (Dist\_Ent\_km), distance to the fjord wall (Dist\_wall\_m), slope of the seabed (Slope), temperature at 19m depth (Temp19) and sea surface temperature (SST0.5) of the top ranked model and models within two AIC points. Displayed are the degrees of freedom (df), AIC values, change in AIC compared to the top model ( $\Delta$ AIC), model weight, adjusted  $R^2$  (Adj  $R^2$ ) and percent deviance explained (% d.e.).

Rank	Model predictors	df	AIC	$\Delta$ AIC	Model weight	Adj $R^2$	d.e. (%)
1	Dist_Ent_km + Dist_wall_m + Slope	11	1032.5	0	0.480	0.113	9.45
2	Dist_Ent_km + Dist_wall_m + Slope + Temp19	12	1034.1	1.59	0.217	0.113	9.49
3	Dist_Ent_km + Dist_wall_m + Slope + SST0.5	12	1034.3	1.85	0.191	0.112	9.48

**Table 3.4.** Statistics for predictor variables included in logistic regression models on presence of bottlenose dolphins in Doubtful Sound. Predictors were present in models that were within two Akaike Information Criterion points of the top model and include: distance from the entrance (Dist\_Ent\_km); distance from the fjord wall (Dist\_Wall\_m); slope (Slope); temperature at 19m depth (Temp19); and sea surface temperature (SST0.5).

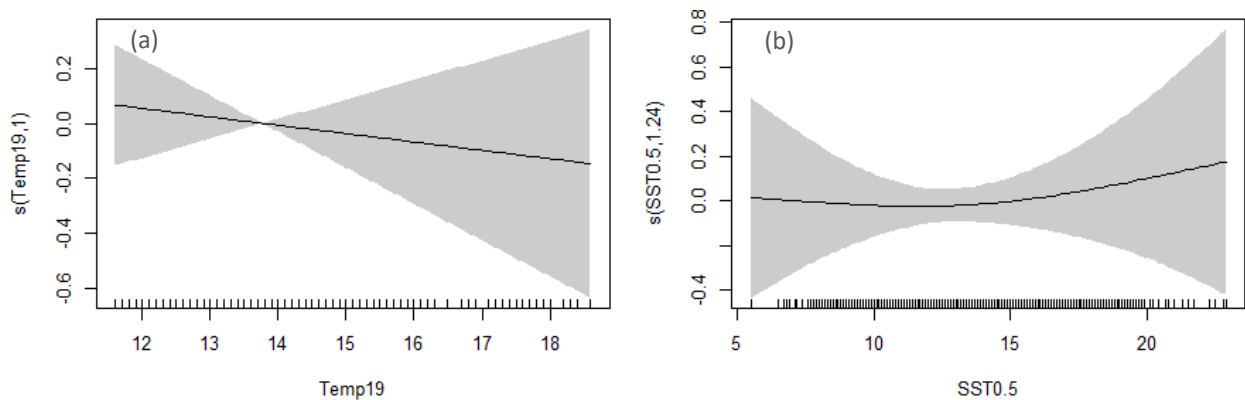
Predictor	Estimated degrees of freedom	Test statistic ( $\chi^2$ )	p-value	Index of Relative Importance
Dist_Ent_km	4.391	80.96	$1.61 \times 10^{-15}$	1
Dist_wall_m	3.598	25.88	$2.88 \times 10^{-5}$	1
Slope	2.618	12.45	0.007	1
Temp19	1.000	0.362	0.547	0.24
SST0.5	1.243	0.405	0.768	0.21

The top ranked model in Doubtful Sound showed that dolphins were most likely to be found around 20km from the fjord entrance, close to the wall and in areas with smaller slope values (Figure 3.2). The number of datapoints for the different values of each predictor variable is represented by the black bar at the bottom of each figure, the more solid means the more points. Fewer datapoints associated with predictors at distances closer than 10km to the fjord entrance (Figure 3.2a); distances farther than 600m from the fjord wall (Figure 3.2b); and slopes with a higher percent change than 150% (Figure 3.2c), are reflected by wider 95% confidence bands on the plots below.



**Figure 3.2.** Effect of explanatory variables from the top ranked logistic generalized additive model on presence of bottlenose dolphins in Doubtful Sound using data from 2005 to 2018. The 95% confidence interval of the response is represented by the shaded area. The y-axes shows the smooth function of each variable, with the estimated degrees of freedom. (a) distance to the entrance (Dist\_Ent\_km), (b) distance to the nearest fjord wall (Dist\_Wall\_m), (c) slope of the seabed as percent change (Slope).

For data collected in Doubtful Sound the second and third ranked models were within two AIC points of the top model (Table 3.3). These models may be competitive with the top model and it is useful to display the relationship of each additional predictor variable with the response (Figure 3.3). The probability of finding dolphins decreased with increasing temperatures at depth (Figure 3.3a). This relationship was linear and the wide 95% confidence bands incorporated zero (and positive) slopes. For SST the relationship with the smoothed response was weak, but overall slightly positive (Figure 3.3c). However, there are wide 95% confidence bands especially at values below 10°C and above 16°C, and this relationship does not seem to be particularly informative.



**Figure 3.3.** Effect of explanatory variables that were included in logistic generalized additive models within two AIC points of the top model on presence of bottlenose dolphins in Doubtful Sound using data from 2005 to 2018. Explanatory variables are additional to the predictors included in the top model. The 95% confidence interval of the response is represented by the shaded area. The y-axes shows the smooth function of each variable, with the estimated degrees of freedom. (a) temperature at 19m depth (Temp19), (c) sea surface temperature taken at 0.5m depth (SST0.5).

### 3.3.2 Model Selection and Results - Dusky Sound

The top ranked model for Dusky Sound included the predictors of distance to the entrance, distance to the wall and aspect (Table 3.5). Distance from the wall and distance from the entrance were present in all models within two AIC points of the top model. Aspect was also included in the second ranked model which also included slope as a predictor variable. The deviance explained was relatively low for all models (less than 6%). Only distance from the wall and entrance were statistically significant in explaining distribution, and were of equal importance to each other ( $\chi^2$  p-value < 0.05, IRI = 1; Table 3.6).

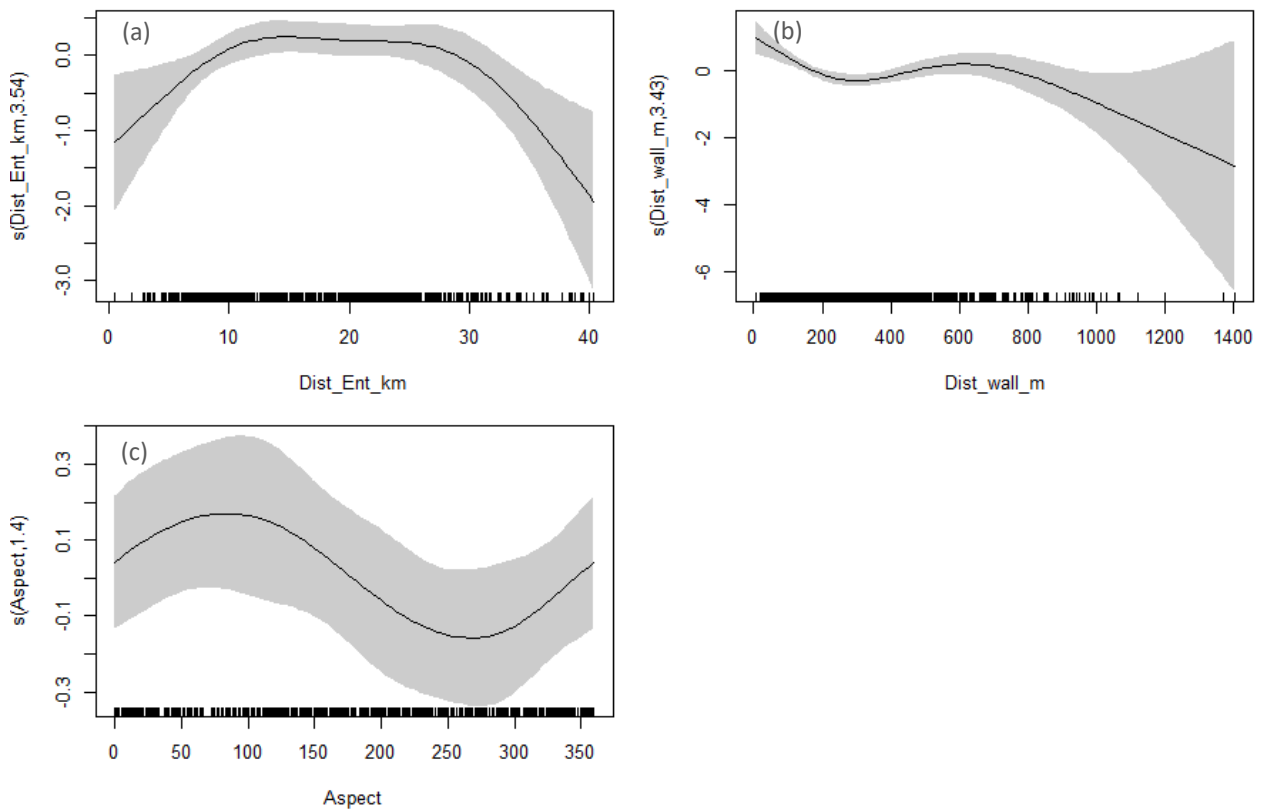
**Table 3.5.** Statistics and ranks of logistic regression models on presence of bottlenose dolphins in Dusky Sound. Models are ranked by Akaike Information Criterion (AIC). Included are the predictors, distance to the fjord entrance (Dist\_Ent\_km), distance to the fjord wall (Dist\_wall\_m), the seabed aspect (Aspect) and slope of the seabed (Slope) of the top ranked model and models within two AIC points. Displayed are the degrees of freedom (df), AIC values, change in AIC compared to the top model ( $\Delta$ AIC), model weight, adjusted  $R^2$  (Adj  $R^2$ ) and percent deviance explained (% d.e.).

Rank	Model predictors	df	AIC	$\Delta$ AIC	Model weight	Adj $R^2$	d.e. (%)
1	Dist_Ent_km + Dist_wall_m + Aspect	9	1002.3	0	0.392	0.055	5.03
2	Dist_Ent_km + Dist_wall_m + Aspect + Slope	11	1003.3	1.10	0.230	0.056	5.27
3	Dist_Ent_km + Dist_wall_m	7	1004.1	1.84	0.156	0.051	4.55

**Table 3.6.** Statistics for predictor variables included in logistic regression models on presence of bottlenose dolphins in Dusky Sound. Predictors were present in models that were within two Akaike Information Criterion points of the top model and include: distance from the entrance (Dist\_Ent\_km); distance from the fjord wall (Dist\_Wall\_m); slope of the seabed (Slope); aspect of the seabed (Aspect).

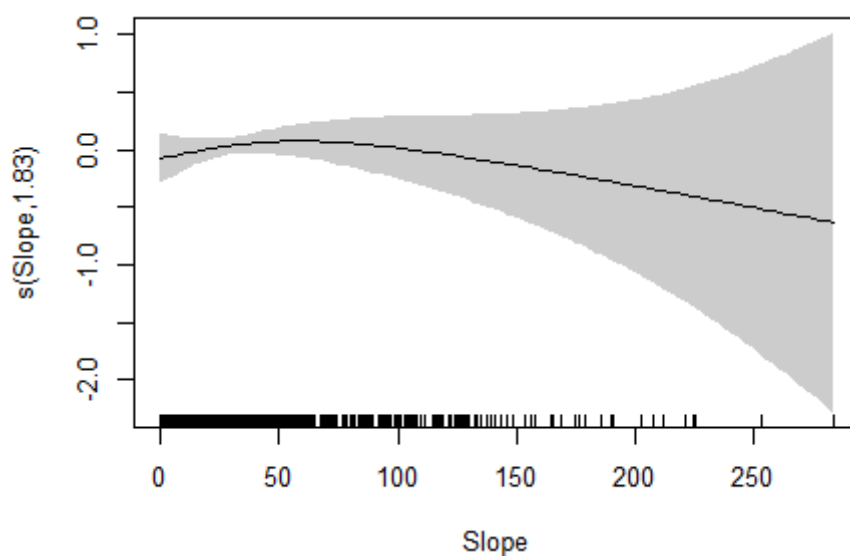
Predictor	Estimated degrees of freedom	Test statistic ( $\chi^2$ )	p-value	Index of Relative Importance
Dist_Ent_km	3.537	18.47	$9.33 \times 10^{-4}$	1
Dist_wall_m	3.430	19.93	$3.32 \times 10^{-4}$	1
Aspect	1.400	3.25	0.090	0.79
Slope	1.833	1.951	0.533	0.28

Smoothed response curves for the top model in Dusky Sound (Figure 3.4) show that the probability of finding dolphins is highest between 10 and 30km from the entrance, close to the wall, and in areas with a north-east aspect. Confidence bands are widest within 5km and greater than 30km to the fjord entrance reflecting areas with fewer data points. The probability of finding dolphins increased at approximately 400m from the wall, and a slight increase was observed again at approximately 600m from the wall, however datapoints become sparse after this point and the general trend is decreasing.



**Figure 3.4.** Effect of explanatory variables from the top ranked logistic generalized additive model on presence of bottlenose dolphins in Dusky Sound using data from 2009 to 2018. The 95% confidence interval of the response is represented by the shaded area. The y-axes show the smooth function of each variable, with the estimated degrees of freedom. (a) distance to the entrance (Dist\_ent\_km), (b) distance to the nearest fjord wall (Dist\_wall\_m), (c) aspect of the seabed (Aspect).

The second best model ( $\Delta AIC = 1.10$ ) included all of the predictor variables in the top model, as well as slope (Table 3.5). The relationship between the smoothed response and slope is initially flat out to a change in slope of about 150%, after this the relationship is negative but the very wide 95% confidence bands reflect the sparse data (Figure 3.5). This means the probability of finding dolphins varied little at slopes below 150% and then decreased after this point.



**Figure 3.5.** Effect of the explanatory variable, slope of the seabed as a percent change (Slope) that was included in the second ranked logistic generalized additive models (within two AIC points) of the top model on presence of bottlenose dolphin in Dusky Sound using data from 2009 to 2018. Explanatory variable is additional to the predictors included in the top model. Ninety-five percent confidence interval of the response is represented by the shaded area. The y-axis shows the smooth function of each variable, with the estimated degrees of freedom.

### 3.4 Discussion

I used Species Distribution Models to investigate the importance of a range of environmental variables in explaining the distribution of bottlenose dolphins in Doubtful and Dusky Sounds. The top models suggest that in both Doubtful and Dusky Sounds dolphins preferred areas that were at middle distances from the fjord entrance and close to the fjord wall. Additionally, in Doubtful Sound dolphins also appeared to prefer areas that were less steep and in Dusky Sound areas that had a north-east aspect. Although none of the models in this study explained more than 10% of the deviance, the predictors included in the top model provide evidence of environmental variables having at least a weak influence on the distribution of dolphins. The results of this study can provide limited insights into the ecology of bottlenose dolphins, but also highlights that some important predictors may be missing. Each abiotic predictor may be directly influencing the distribution of the dolphins, but in most cases, it is more likely that they are acting as proxies for biotic interactions. In most studies of habitat use by cetaceans, researchers generally agree that biotic factors are probably most important, but are difficult to measure (e.g. Torres et al. 2008).

Distance from the fjord entrance is representative of the strong environmental gradients, particularly salinity and temperature, present throughout the fjords (Stanton and Pickard 1981). In both Doubtful and Dusky Sounds there is a preference for areas closer to middle of the fjords. This preference may be due to the dolphins using areas that impose less physiological cost; for example the inner fjord is a less saline environment. Dolphins showed higher levels of epidermal diseases when exposed to lower salinity (Wilson et al. 1999; Rowe et al. 2010). In Doubtful Sound, where there is a more defined peak in preferred distance from the entrance, dolphins experience a much higher freshwater influence (due to the tailrace) and show four times the incidence of skin lesions than dolphins in Dusky Sound (Rowe et al. 2010). Although it would have been better to include salinity as a predictor, as was done with temperature, this was not possible with the long term dataset.

The other predictors included in the top model may be attributed to foraging opportunities for the dolphins. The fjord walls certainly represent areas of higher primary productivity (Grange 1991; Matthews and Heimdal 1979) and the dolphins in Doubtful Sound, at least, predominantly eat reef-associated fish (Lusseau and Wing 2006). Therefore, the dolphins would have better access to foraging grounds when at a closer proximity to the fjord wall. Areas near the wall with less slope may accumulate fallen rocks and detritus which provide



more habitat complexity. Many species of fish have been shown to prefer areas with greater habitat complexity (Chittaro 2004). Due to the steep topography of Fiordland, it is a common occurrence for rock fall or terrestrial material to fall into the water. In fact the breakdown of this terrestrial matter provides a major source of primary productivity fuelling some of the marine benthic systems within Fiordland (McLeod and Wing 2007). Areas with a north-east aspect likely receive higher solar radiation (Cornelisen et al. 2007) and thus, would also have higher primary productivity.

Interestingly, depth and distance to the wall had high concavity, leading to the exclusion of one of these predictors from the models. Depth proved to be a worse predictor in the models than distance to the wall, therefore access to the wall environment may be more important in explaining distribution than access to the seabed. An alternative explanation is that distance to the wall is acting as a proxy for depth, which would be expected to be important. This could be especially so for the dolphins in Doubtful Sound, which predominantly eat reef associated fish; the deeper they have to dive the greater the physiological cost (Williams et al. 1999). Distance to the wall may encompass depth as a predictor, or the spatial resolution of the models, and the depth layer used, may have failed to accurately represent the true response to the bathymetry.

The above discussed predictors were all included in either the top habitat models for the dolphins of Doubtful Sound (e.g. slope), Dusky Sound (e.g. aspect) or both (e.g. distance to the wall or entrance). Models within two AIC points of the top model had similar performance, so it would be poor practice to ignore additional information provided by these models (Burnham et al. 2011). Slope was included in the second ranked model in Dusky Sound. The relationship this predictor had with dolphin distribution was similar to the relationship from the top model in Doubtful Sound, except that the trends were weaker. For example, in Dusky Sound dolphins seem to avoid areas with steeper slopes, rather than preferring areas with less slope. The other predictors included in models within two AIC points of the top model were only present in the Doubtful Sound models, and were both related to temperature.

Temperature is thought to be one of the most significant factors for the bottlenose dolphins in Fiordland due to living near to the southern extreme of their range (Schneider 1999; Henderson 2013; Ch. 2). However, the results from this study suggest that the dolphins do not prefer areas of warmer water temperature, either at the surface or at 19m depth. Although these results are contrary to interpretations of previous research, this study is the first analysis to combine

several variables in one model. This suggests that the seasonal changes and variation in habitat use are driven by something other than temperature. Alternatively, the temperature data used in this study may not have been at the appropriate spatial resolution to elucidate the real effect. Henderson (2013) tested the data from the oceanographic mooring buoys throughout the fjord and found no correlation with sightings and temperature at depth, however there was a correlation with SST. This is likely because Henderson's SST data were very fine-scale, recorded every 10 seconds while surveying the fjord. The oceanic mooring buoys undoubtedly help to describe broad temperature variation throughout the fjord, however, for future studies of habitat use it would be better to continuously collect SST data during dolphin surveys.

The low explanatory power of the SDMs in this study suggest that the abiotic variables are not the predominant drivers of dolphin distribution in Fiordland. For models of dolphin distribution in Dusky Sound, the low deviance explained, as well as the suggested lack of fit from residual tests, further suggest that important predictors were missing from the dataset. This may have been due to the resolution of some of the data, such as temperature, or because these variables explain only some of the variation in more important biotic variables, such as prey availability. For the bottlenose dolphins of Fiordland, abiotic predictors seem to be, at best, poor proxies for biotic variables. Incorporating prey distribution data into SDMs may help to elucidate the role biotic variables have on bottlenose dolphin distribution and is investigated in chapter four.

## Chapter 4

### Influence of biotic variables in habitat models of bottlenose dolphins in Doubtful Sound

#### 4.1 Introduction

The distribution of an organism, population or species is determined by a combination of complex interactions with abiotic and biotic factors (Hutchinson 1957). For predatory species it is likely that the distribution of prey, which is strongly influenced by the environment, is very important (Hugie and Dill 1994; Torres et al. 2008). Many studies of habitat use by top predators use abiotic predictor variables as proxies for prey distribution (e.g. Klar et al. 2008; Azzellino et al. 2008; Valeix et al. 2009; Pirotta et al. 2011; Azzellino et al. 2012; Hartel et al. 2015). Such environmental variables are easier to sample, can often be applied retrospectively to distribution data, and can provide useful insight about biotic interactions (see McArthur et al. 2010 for a review). Ecological relationships, however, are complex. Simplifying the influence that prey have on predators, to correlations that predators have with the environmental variables, is likely to obscure important ecological functions and relationships.

It is often difficult to sample prey at the appropriate spatial or temporal scale to obtain accurate information on how they influence the habitat use of a predator. This seems to be particularly so for marine mammal predators, and is why few studies have attempted to incorporate prey data in studies of habitat use (for exceptions see Heithaus and Dill 2002, 2006; Torres et al. 2008). Even when appropriate data on prey are collected, the effect of biotic variables can be difficult to demonstrate (Torres et al. 2008).

For odontocetes, fish generally form the main prey source, though cephalopods can be extremely important (Santos et al. 2001; De Pierrepont et al. 2005). A range of methods are available to sample and quantify the distribution and abundance of odontocete prey, including angling, trawling, hydro-acoustic surveys, underwater visual census, and underwater video (Willis et al. 2000; Torres et al. 2008; Lawrence et al. 2016). Each method has pros and cons, and different methods are best suited to specific prey. In the case of pelagic fish, hydro-acoustic surveys or midwater trawls are often used (Lawson et al. 2001; Lawrence et al. 2016). Abundance and distribution estimates of benthic fish can be obtained with trawling, and other fishing methods are often used (Willis et al. 2000). These extractive methods, such as trawling, potting or angling, allow for physical measurement, tissue sampling and unambiguous identification of species, however, they can damage and kill the target species and/or harm the

environment. Additionally, extractive methods may not be appropriate for endangered species or working within protected areas (e.g. marine reserves). Visual methods, such as line transect scuba surveys or video, can provide an alternative; prey species can be identified and quantified, and in some cases estimating prey sizes is also possible (Willis et al. 2000; Mallet and Pelletier 2014). These methods, however, attract certain species but repel others. Baited Underwater Video (BUV) provides a non-invasive method of sampling fish abundances and distribution. Because BUV deployments are typically quite short (usually between 30-60 minutes), multiple samples can be taken on the same day over a large area (Willis and Babcock 2000; Zintzen 2016). This can allow for spatial data to be collected at high resolution, which is particularly useful for studies of highly mobile predators such as bottlenose dolphins.

Fiordland bottlenose dolphins are thought to live near their physiological temperature limit, as they reside near the southernmost point of global bottlenose dolphin range. Because of this, it is thought that the environment of Doubtful Sound directly influences habitat use (Schneider 1999; Henderson 2013). The dolphins also need to meet the physiological costs of living in a cool environment by obtaining sufficient food. Models explaining the distribution of bottlenose dolphins in Fiordland have not yet incorporated biotic factors. The mostly resident population of bottlenose dolphins in Doubtful Sound presents an opportunity to study the distribution of a top predator while concurrently collecting data on the distribution of their prey. The only study of dietary preferences of bottlenose dolphins in Fiordland indicated they rely primarily on rocky-reef associated fish (Lusseau and Wing 2006). Therefore, quantifying the relative abundance and distribution of bottlenose dolphin prey should focus primarily on the steep rock walls of the fjord.

This chapter investigates the role of biotic variables on habitat use of bottlenose dolphins in Doubtful Sound during 2018. Species Distribution Models (SDMs) were constructed, and the influence of biotic variables, collected with BUV, on model performance was evaluated. This study should enable a better understanding of what drives habitat use of bottlenose dolphins in Fiordland, and provide valuable insights for managing these populations in the future.

## 4.2 Methods

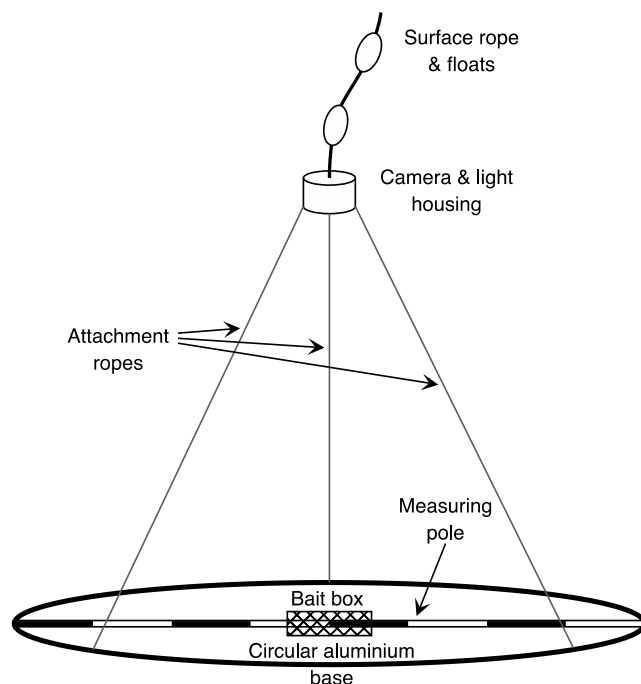
### 4.2.1 Field methods

#### *Bottlenose dolphin surveys*

Photo-ID surveys for bottlenose dolphins were conducted in Doubtful Sound over three week periods during each season in 2018: summer (January-February), autumn (March-April), winter (June) and spring (October-November). Field methods were consistent with the standardised surveys described in chapter two.

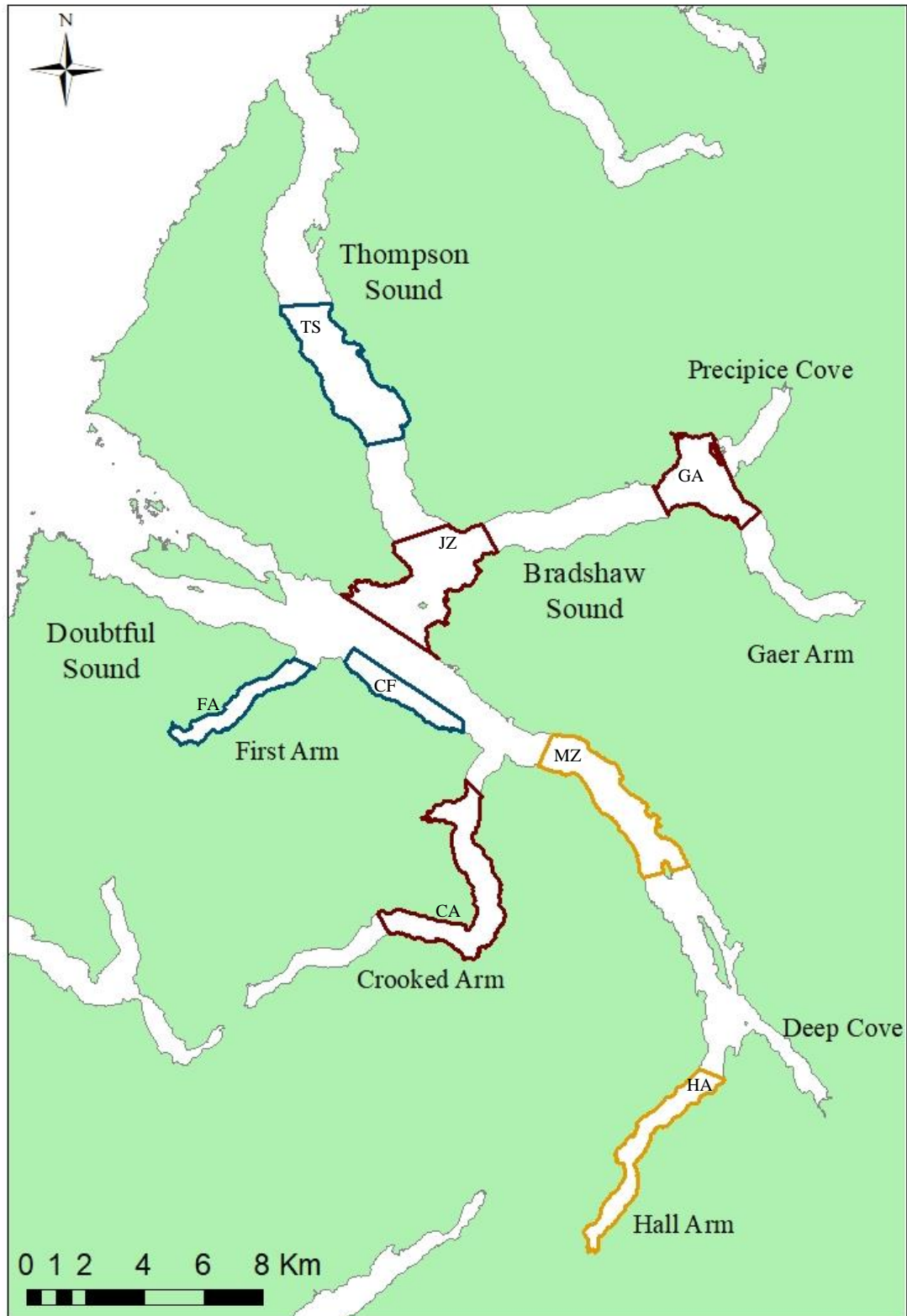
#### *Baited Underwater Video*

To collect relative abundance and distribution data on potential prey species of bottlenose dolphins, I conducted BUV surveys concurrently with the dolphin surveys. BUVs consisted of a video camera and light source attached to a frame facing a bait box fixed to the centre of a 1m long measuring pole (Figure 4.1). A circular base was used to ensure the BUV would be positioned away from the steep fjord wall. Videos were recorded at 1080p (60 fps) using a GoPro Hero 5 action camera, contained within an underwater housing rated to 60m. The bait box was stocked with four anchovies, which were replaced for each deployment. Anchovies were used due to their oily composition, and because they have proved successful in other similar studies (e.g. Wraith et al. 2013). The light source was a Knog qudos action light, set to wide angle and low power. This was sufficient to illuminate and identify all fish species that entered the camera's field of view.



**Figure 4.1.** Example schematic of Baited Underwater Video (BUV) structure used throughout Doubtful Sound in 2018 for surveys of relative abundance and diversity of fish.

BUVs were deployed in eight survey zones within Doubtful Sound during 2018 (Figure 4.2). The extent and placement of each zone represents a general area of high, medium or low use by bottlenose dolphins, based on habitat use described in chapter two (see also Henderson 2013). Additionally, the survey zones were spread around Doubtful Sound to provide representative coverage of different habitats from the inner to outer fjord. Due to the size of Doubtful Sound, I attempted to survey each zone at least ten times every season, essentially once every two days. BUV deployments were standardised to a 30 minute time period, from when the BUV reached the bottom (e.g. Willis and Babcock 2000). Suitable areas for deployment were defined as relatively flat sections of benthos between 10m and 40m deep, because previous research has shown that dives by bottlenose dolphins in Doubtful Sound were most frequent to these depths (Schneider 1999). BUVs deployed on the same day were spaced at least 400m apart to minimise any chance of interference. This follows Department of Conservation (DOC) guidelines to avoid sampling the same fish in replicate BUV videos (Cappo et al. 2004; Zintzen 2016). For each zone, a suite of potential survey points were randomly generated in ArcMAP v10.6.1 (ESRI; Environmental Systems Research Institute, Redlands, California, USA). Potential points were sometimes outside the desired depth range, or on slopes too steep for the BUV to remain in place. In that case I would drive the research vessel in a straight line towards the fjord wall until a suitable depth was found. If no such area could be found, this deployment point would be abandoned, and I would move on to the next randomly generated point. These criteria resulted in surveying a range of benthic habitat, including areas of coarse sediment, fine sediment, kelp, boulders and bedrock. Any videos recorded on an extreme angle, which had an obscured field of view, or had errors in the recording process were removed from further analysis.



**Figure 4.2.** Baited Underwater Video survey zones in Doubtful Sound, sampled during 2018. Colours represent use by bottlenose dolphins: blue = low use, yellow = medium use, and maroon = high use. Letter codes represent zone names: HA (Hall Arm), MZ (inner main channel), CA (Crooked Arm), CF (between Crooked and First Arms), JZ (Junction), GA (Gaer Arm) and TS (Thompson Sound).

#### 4.2.2 Data Analysis

##### *Baited underwater video analysis*

I analysed all videos for the presence of fish, rock lobster (*Jasus edwardsii*) and octopus (*Macropus maorum*), and counted the maximum number (*maxN*) of each species present during each standardised 30 minute video. *MaxN* (a relative abundance estimate) is defined as the maximum number of individuals from one species in the frame at any time during the video (Cappo et al. 2007). To ensure *maxN* was accurate each minute of the video was analysed separately, and the highest estimate was taken for further analysis. This method likely produces a conservative estimate of relative abundance, but prevents an individual from being counted multiple times if it re-enters the frame (Willis and Babcock 2000). The majority of fish (>97%) could be identified to species. The few that could not (mostly due to their small size) were excluded from further analyses.

Generally, dolphins are considered to be opportunistic foragers, consuming a wide variety of prey based on availability (e.g. Wells and Scott 1999). Because of this, I decided to incorporate only the most prevalent potential prey species observed in Doubtful Sound, as they would likely be more available for consumption by the dolphins. The most prevalent species were chosen based on the average *maxN* of all videos and the proportion of videos in which they occurred. Species that occurred in over 30% of videos were chosen for further analysis, and include spotty (*Notolabrus celidotus*), sea perch (*Helicolenus percoides*), butterfly perch (*Caesioperca lepidoptera*), scarlet wrasse (*Pseudolabrus miles*), girdled wrasse (*Notolabrus cinctus*), tarakihi (*Nemadactylus macropterus*) and blue cod (*Parapercis colias*). As it is likely that dolphins are not targeting one specific species in Doubtful Sound, I summed *maxN* estimates of the five species with the highest relative abundance (spotty, sea perch, butterfly perch, scarlet wrasse and girdled wrasse) to gain a general abundance estimate of fish per video (*abunT5*). Diversity estimates for each video were also calculated, using the Shannon diversity index (Shannon 1948). The diversity index, *abunT5* and relative abundance of each of the seven most prevalent species were used as biotic predictors in the SDMs.

#### 4.2.3 Species Distribution Modelling

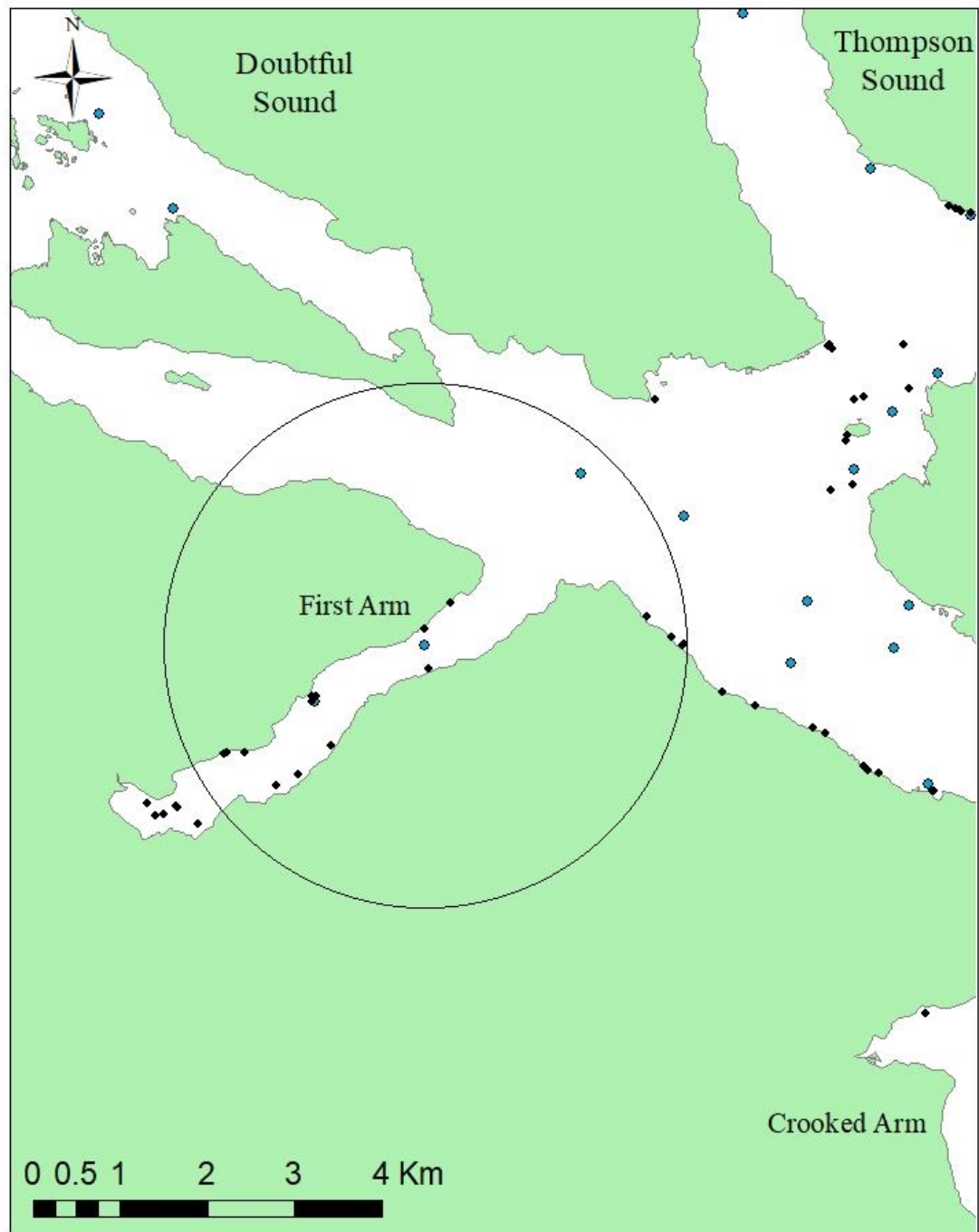
I used Generalised Additive Models (GAMs) to investigate the role of potential prey in the distribution of bottlenose dolphins during 2018. To do this I compared model performance between GAMs containing only abiotic predictor variables, and GAMs containing both abiotic



and prey predictors. GAMs, with a logit link function, were developed in the R environment (R Development Core Team 2018) using the package “mgcv” (Wood 2017). As in chapter three, a binary response of bottlenose dolphin presence and pseudo-absence was related to a suite of predictor variables. Thin-plate regression splines were applied to continuous predictor variables, limited to a maximum of five degrees of freedom (k) to reduce the risk of overfitting (e.g. Marubini et al. 2009; Rayment et al. 2015). Chapter three provides detailed methodology on how the response variable and abiotic predictor variables were generated, and how the predictor variables were applied to each response. The details are not repeated here, however it should be noted that only data collected during 2018 were used for the models produced in this chapter, because BUV data were available only from 2018.

#### *Biotic Predictor Variables*

Because the BUV surveys did not necessarily occur at the dolphin presence and pseudo-absence points, I developed a method to assign the biotic predictor values to the response variable locations. Inverse Distance Weighting (IDW) allowed for a value of a variable to be assigned to any location in space based on proximity to known values of that variable. The closer a point is to the target the more it influenced the final estimate. Biotic predictor variables were assigned to each bottlenose dolphin presence and pseudo-absence point using “idw” from the “gstat” package (Pebesma 2004; Gräler et al. 2016) in R studio. A search radius of 3km from the response variable was used to interpolate BUV values within this area (Figure 4.3). This prevented BUV values separated by land masses from being interpolated, while enabling an estimate for prey that was potentially accessible to the dolphins. Only BUVs deployed in the same season as the dolphin sighting were used for interpolation.



**Figure 4.3.** Example search radius (3km) around one bottlenose dolphin location point (blue point) in Doubtful Sound during 2018. Values from baited underwater video surveys (black points) within the search radius (black circle) for this bottlenose dolphin location were interpolated through inverse distance weighting.

### *Model Selection*

In chapter three, occurrence data for bottlenose dolphins in Doubtful Sound were collected between 2005 and 2018. A suite of abiotic predictor variables were modelled against the smoothed response of presence and absence. Predictors that had pairwise concurrency values greater than 0.3 were retrospectively excluded from being in the same models together (He et al. 2006). Akaike's Information Criterion (AIC; Akaike 1973) was used to choose the best fitting model with the least complexity. The predictors included in the final top model in chapter three were: distance from the entrance (Dist\_ent\_km), distance from the fjord wall (Dist\_wall\_m) and the percent change in slope (Slope). These predictors were used to create an abiotic model of the distribution of bottlenose dolphins in Doubtful Sound for 2018. Co-opting the top predictor variables chosen in chapter three was considered more appropriate than repeating the model selection process with the 2018 subset of data. This is because model selection with long-term occurrence data incorporated more distribution information and the choice of final predictor variables should therefore be more robust. To ensure it was appropriate to include these predictors in a model for 2018, pairwise concurrency was checked.

I used the final abiotic-only model as a template to include the biotic predictor variables. This allows direct comparison between models with only environmental habitat characteristics and with a mix of environmental and prey predictors. All available biotic predictor variables were added to the model and pairwise concurrency was compared. As in chapter three, predictors with pairwise concurrency values greater than 0.3 were not included in the same model together (He et al. 2006). Univariate GAMs were created for each correlated predictor variable, and the one that had the highest model deviance explained was used in further models. Models were compared with backwards stepwise selection and the model with the lowest AICc value (Akaike's Information Criterion corrected for small sample size; Hurvich and Tsai 1989) was chosen as the top model. Similarly to chapter three models within two AICc points of the top model were ranked in R using the dredge function in the "MuMIn" package (Barton 2018). Models within two AICc points are considered to have similar performance to the top model, it is therefore good practice to include the additional information contained within (Burnham et al. 2011). The relative performance of the abiotic model and the top model incorporating prey variables was judged by comparing AICc values and the percentage deviance explained.

To compare predictor variables, the index of relative importance (IRI) was calculated for predictors included in the top model and those within two AIC points. This was completed as described in chapter three, using model averaging with the "MuMIn" package in R.

### *Residual checks*

As in chapter three, residuals of the abiotic and final biotic models were checked to ensure that the data met model assumptions. Initially “gam.check” was used to ensure that limiting the smoothed predictor variables to a maximum of five degrees of freedom (k) did not over-smooth the variables. Due to the difficulty in interpreting diagnostic plots for a binary response (Landwehr et al. 1984; Zuur et al. 2009), however, I checked residuals with a simulation technique from the package “DHARMA” (Hartig 2019), as described in chapter three (for residuals see Appendix 9; 10).

### *Spatial autocorrelation*

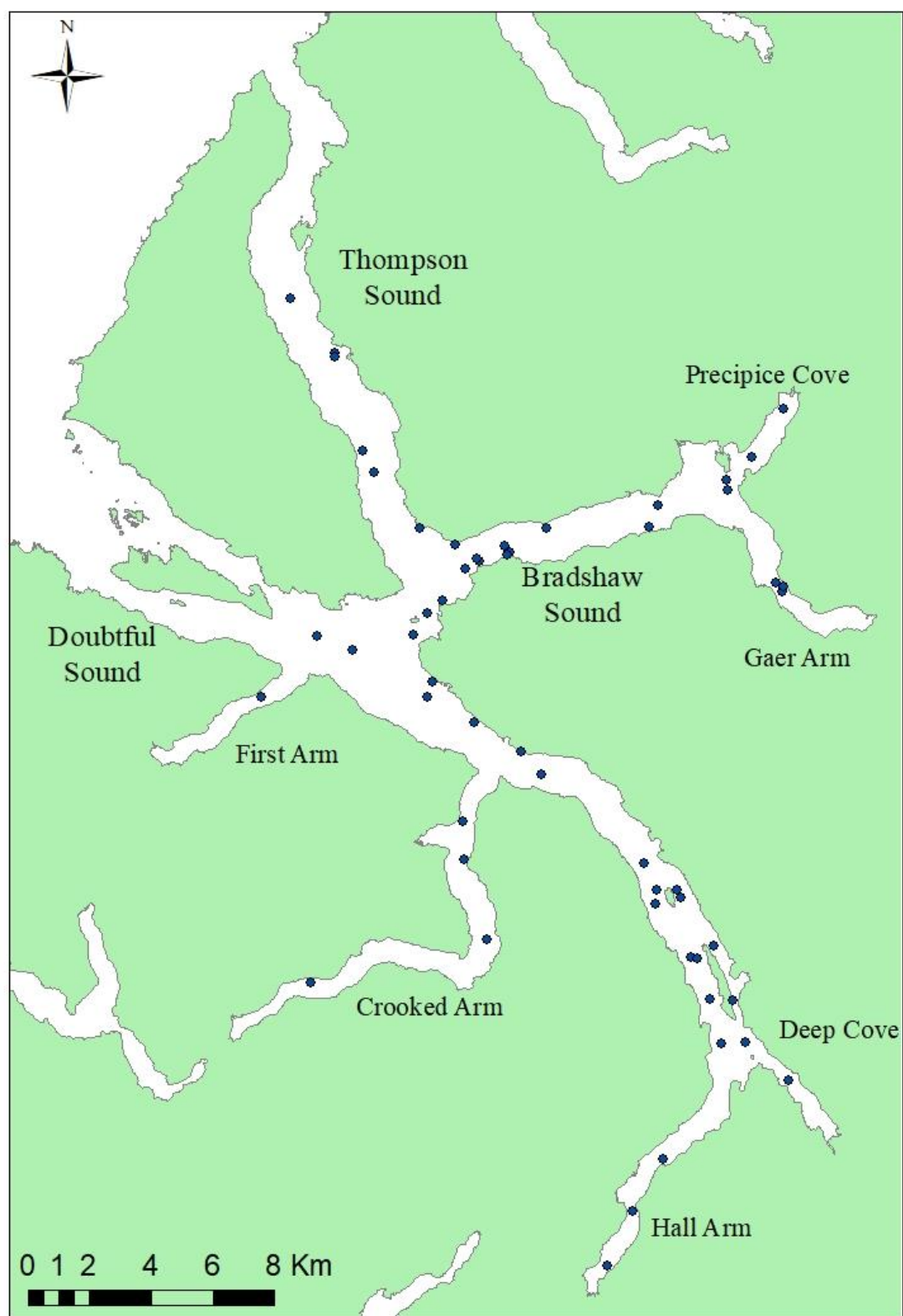
As described in chapter three, I attempted to reduce spatial autocorrelation (a measure of similarity as a function of distance) by excluding subsequent sightings on the same day of the same group of dolphins. Spatial autocorrelation between data points, however, can also be tested statistically using correlograms (Bjørnstad and Falck 2001; Zuur et al. 2009). This was completed using the package “ncf” in R (Bjørnstad 2018). Spatial autocorrelation was not an issue for either model (Appendix 11, 12).

## **4.3 Results**

The distance surveyed and the number of dolphin groups observed varied among seasons. When sightings were standardised by survey effort (km), summer had the highest sighting rate and spring had the lowest (Table 4.1). Most sightings occurred in the main channels of Doubtful Sound, Thompson Sound and Bradshaw Sound, though there were occasional sightings in the upper arms of the fjord (Figure 4.4).

**Table 4.1.** Summary table for both bottlenose dolphin group sightings and surveys in Doubtful Sound during 2018. Sightings are standardised by survey effort, in this case the number of dolphin group sightings for each km surveyed.

Season	Distance Surveyed (km)	Bottlenose dolphin groups	Standardised Sightings/km surveyed
Summer	3009.3	23	0.0076
Autumn	1735.2	10	0.0058
Winter	1468.8	9	0.0061
Spring	2750.2	12	0.0044
<b>Total</b>	<b>8963.6</b>	<b>54</b>	<b>0.0060</b>



**Figure 4.4.** Point locations of bottlenose dolphin groups sighted in Doubtful Sound during 2018.

A total of 422 BUV surveys were conducted throughout Doubtful Sound during 2018. Of these 323 videos were of sufficient quality to be used for further analysis. Summer had the highest number of deployments, while autumn had the least (Table 4.2). At least five replicate BUV surveys could be used for estimates of relative fish abundance and diversity in each zone for each season (Table 4.2), resulting in good survey coverage of Doubtful Sound (Figure 4.5).

**Table 4.2.** Number of baited underwater video deployments in each survey zone in Doubtful Sound during 2018. Survey zones are: Hall Arm (HA), Crooked Arm (CA), First Arm (FA), Junction (JZ), entrance to Gaer Arm (GA), Thompson Sound (TS) Crooked Arm to First Arm (CF) and the inner main area in Doubtful Sound (MZ). The total number of videos is given for each study zone and season.

Season	Number of Deployments								Total
	HA	CA	FA	JZ	GA	TS	CF	MZ	
Summer	13	9	12	12	15	12	10	11	<b>94</b>
Autumn	8	5	7	9	7	9	7	6	<b>58</b>
Winter	9	13	11	12	12	13	11	11	<b>92</b>
Spring	10	10	11	11	8	8	11	10	<b>79</b>
<b>Total</b>	<b>40</b>	<b>37</b>	<b>41</b>	<b>44</b>	<b>42</b>	<b>42</b>	<b>39</b>	<b>38</b>	<b>323</b>



**Figure 4.5.** Location of Baited Underwater Video (BUV) deployments in Doubtful Sound during 2018. Colours represent the season of deployment: yellow = summer, orange = autumn, blue = winter and green = spring.

Twenty-six species were identified and counted from BUV surveys taken in Doubtful Sound during 2018 (Table 4.3). Seven species were each observed on  $\geq 100$  videos, including spotty, sea perch, butterfly perch, scarlet wrasse, girdled wrasse, blue cod and tarakihi. The prevalence of species was standardised and compared by the proportion of videos they featured in. This revealed that the top seven species were observed in a much greater proportion of videos than the remaining 22 ( $>0.3$  of all videos compared to  $<0.1$ ; Table 4.3). Small sharks were the next most frequent group observed in Doubtful Sound using BUV.

**Table 4.3.** Frequency and relative abundance (*maxN*) of species observed in Baited Underwater Video (BUV) surveys in Doubtful Sound during 2018. Species are ranked by proportion of videos they occur in.

Common name	Scientific name	# of videos observed in	Proportion of videos	Mean maxN	Std. error
Spotty	<i>Notolabrus celidotus</i>	265	0.820	7.45	$\pm 3.84$
Jock Stewart	<i>Helicolenus percoides</i>	201	0.622	6.76	$\pm 3.50$
Tarakihi	<i>Nemadactylus macropterus</i>	162	0.502	3.09	$\pm 1.82$
Scarlet wrasse	<i>Pseudolabrus miles</i>	161	0.498	4.25	$\pm 2.33$
Bluecod	<i>Parapercis colias</i>	157	0.486	3.09	$\pm 1.82$
Butterfly Perch	<i>Caesioperca lepidoptera</i>	104	0.322	6.91	$\pm 3.56$
Girdled wrasse	<i>Notolabrus cinctus</i>	100	0.310	6.89	$\pm 3.55$
Spiny dogfish	<i>Squalus acanthias</i>	28	0.087	2.76	$\pm 1.60$
School shark	<i>Galeorhinus galeus</i>	16	0.050	1.88	$\pm 1.21$
Carpet shark	<i>Cephaloscyllium Isabella</i>	13	0.040	2.00	$\pm 1.22$
Southern bastard cod	<i>Pseudophycis barbata</i>	11	0.034	2.17	$\pm 1.24$
Sevengill shark	<i>Notorynchus cepedianus</i>	10	0.031	1.82	$\pm 1.11$
Spiny lobster	<i>Jasus edwardsii</i>	9	0.028	3.40	$\pm 1.65$
Hagfish	<i>Eptatretus cirrhatus</i>	7	0.022	2.80	$\pm 1.14$
Leatherjacket	<i>Parika scaber</i>	6	0.019	1.71	$\pm 0.94$
Red gurnard	<i>Chelidonichthys kumu</i>	5	0.015	1.67	$\pm 0.87$
Scorpionfish	<i>Scorpaena cardinalis</i>	4	0.012	1.60	$\pm 0.77$
Copper moki	<i>Latridopsis forsteri</i>	4	0.012	2.00	$\pm 0.88$
Marblefish	<i>Aplodactylus arcidens</i>	3	0.009	1.50	$\pm 0.63$
Splendid perch	<i>Callanthias allporti</i>	3	0.009	1.50	$\pm 0.63$
Octopus	<i>Macroctopus maorum</i>	3	0.009	1.50	$\pm 0.63$
Rig	<i>Mustelus lenticulatus</i>	2	0.006	2.00	$\pm 0.58$
Northern dogfish	<i>Squalus griffin</i>	2	0.006	1.33	$\pm 0.41$
Rough skate	<i>Zearaja nasutus</i>	1	0.003	1.00	$\pm 0.00$
Trumpeter	<i>Latris lineata</i>	1	0.003	1.00	$\pm 0.00$
Pigfish	<i>Congiopodus leucopaecilus</i>	1	0.003	1.00	$\pm 0.00$



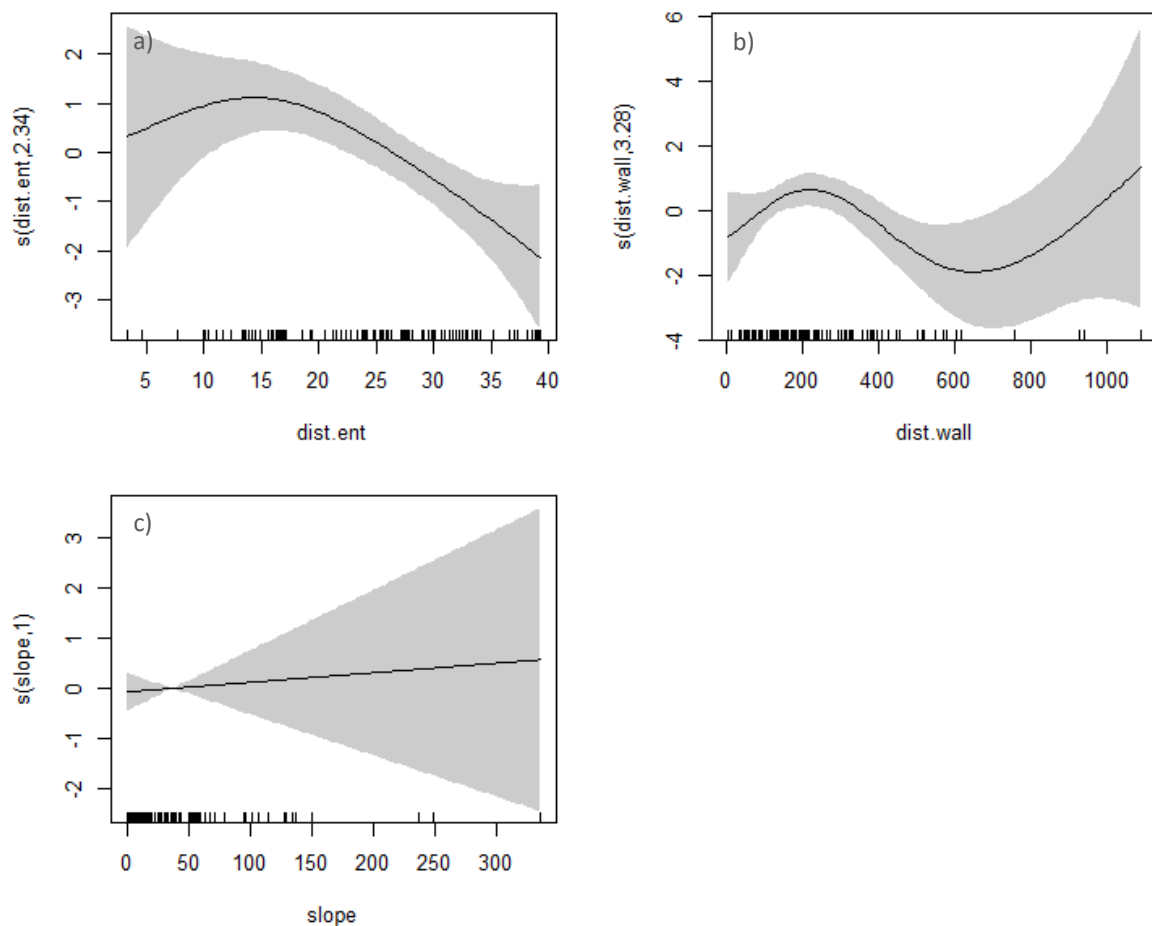
#### 4.3.1 Species Distribution Modelling

None of the abiotic predictor variables included in the species distribution models for 2018 had pairwise concurrency estimates greater than 0.3 (Table 4.4). When biotic predictors were added to the model, distance from the entrance was correlated with several variables, and several biotic predictors were correlated with each other (Table 4.4). Deviance explained in univariate models was compared and the variable that explained the highest deviance was retained (Appendix 13). The predictor variables included in the full biotic model were distance to the fjord wall, percent change in slope, relative abundance of girdled wrasse, spotty, sea perch, tarakihi and bluecod.

**Table 4.4.** Estimated pairwise concurrency for smoothed terms of predictor variables in habitat use models for bottlenose dolphins in Doubtful Sound during 2018: a) distance to the fjord entrance; b) distance to the fjord wall; c) percent change in slope; d) diversity of Baited Underwater Videos (BUVs) measured using Shannon's diversity index; e) combined relative abundance of the most prevalent fish species present in the BUVs; f) relative abundance of spotty (*Notolabrus celidotus*); g) relative abundance of sea perch (*Helicolenus percoides*); h) relative abundance of butterfly perch (*Caesioperca lepidoptera*); i) relative abundance of girdled wrasse (*Notolabrus cinctus*); j) relative abundance of scarlet wrasse (*Pseudolabrus miles*); k) relative abundance of bluecod (*Parapercis colias*); l) relative abundance of Tarakihi (*Nemadactylus macropterus*). Pairwise concurrency estimates greater than 0.3 are displayed in bold.

	a)	b)	c)	d)	e)	f)	g)	h)	i)	j)	k)	l)
a)	1.00	0.22	0.12	<b>0.43</b>	0.16	0.06	0.18	0.27	0.26	<b>0.57</b>	0.12	0.15
b)	0.15	1.00	0.03	0.08	0.01	0.01	0.03	0.02	0.03	0.08	0.02	0.04
c)	0.13	0.03	1.00	0.08	0.05	0.04	0.02	0.08	0.07	0.05	0.04	0.01
d)	<b>0.47</b>	0.08	0.05	1.00	0.09	0.04	0.12	0.11	0.20	<b>0.40</b>	0.22	0.08
e)	0.21	0.03	0.05	0.16	1.00	0.43	0.26	<b>0.46</b>	<b>0.58</b>	0.29	0.06	0.02
f)	0.03	0.04	0.04	0.06	0.41	1.00	0.06	0.07	0.08	0.05	0.07	0.01
g)	0.13	0.04	0.02	0.07	0.15	0.08	1.00	0.05	0.07	0.02	0.06	0.02
h)	<b>0.45</b>	0.16	0.15	0.23	<b>0.50</b>	0.03	0.02	1.00	<b>0.68</b>	<b>0.40</b>	0.03	0.01
i)	<b>0.54</b>	0.13	0.15	<b>0.39</b>	<b>0.53</b>	0.05	0.08	0.59	1.00	<b>0.54</b>	0.06	0.02
j)	<b>0.64</b>	0.08	0.09	<b>0.39</b>	<b>0.31</b>	0.06	0.03	<b>0.40</b>	<b>0.49</b>	1.00	0.16	0.04
k)	0.15	0.06	0.03	<b>0.33</b>	0.06	0.04	0.13	0.04	0.04	0.11	1.00	0.07
l)	0.07	0.03	0.03	0.22	0.01	0.01	0.06	0.01	0.01	0.04	0.09	1.00

The top abiotic model obtained from long term (2005-2018) sightings of bottlenose dolphins in Doubtful Sound was used to investigate distribution patterns for 2018. To aid understanding of the relationship between the physical environment and the dolphins, the smoothed response was modelled against the predictor variables (Figure 4.6). This model indicated that the probability of finding bottlenose dolphins was highest approximately 15km from the fjord entrance and approximately 200m from the fjord wall (Figure 4.6a, b). There was a slight positive linear relationship between dolphin presence and slope, but note that the data were sparse above slopes of 50%, as indicated by the wide confidence limits (Figure 4.6c). Nearly 20% of the deviance in the occurrence of bottlenose dolphins during 2018 was explained with the abiotic model (Table 4.7).



**Figure 4.6.** Effect of explanatory variables from the top ranked logistic generalised additive model, using only abiotic predictors, on presence of bottlenose dolphins in Doubtful Sound during 2018. The 95% confidence interval of the response is represented by the shaded area. The y-axes show the smooth function of each variable, with the estimated degrees of freedom. (a) distance to the entrance (Dist\_ent\_km), (b) distance to the nearest fjord wall (Dist\_wall\_m), (c) slope of the seabed (Slope).

When biotic variables are included in the model selection process, a combination of both abiotic (distance from the fjord wall) and biotic predictors (the relative abundance of girdled wrasse and tarakihi) were included in the top ranked model (Table 4.5). Both girdled wrasse and distance from the fjord wall were included in all models within two AICc points of the top model. The deviance explained by all models with less than a two-point change in AICc was greater than 36% (Table 4.5). Distance to the wall and the relative abundance of girdled wrasse were the most important predictors, but only the relative abundance of girdled wrasse was statistically significant (Table 4.6).

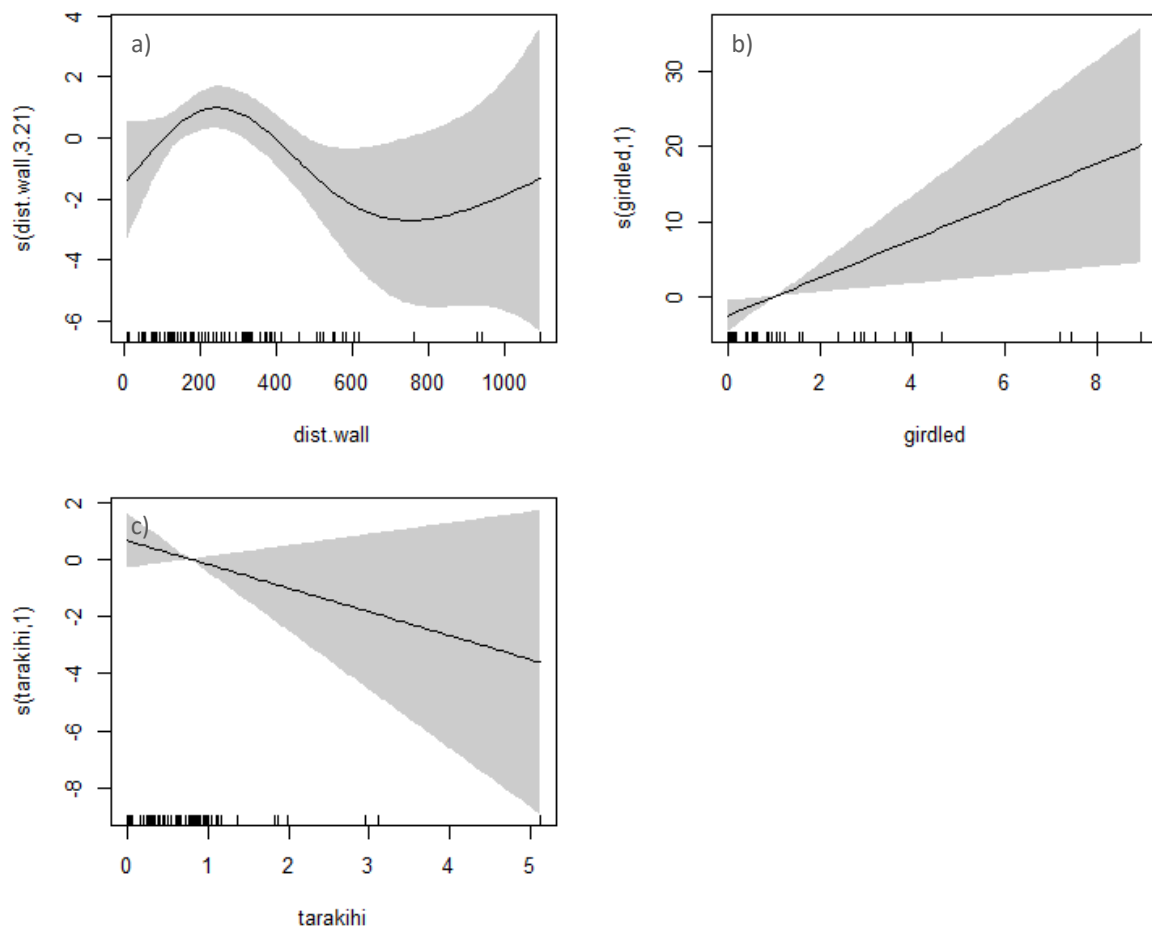
**Table 4.5.** Statistics and ranks of logistic regression models on presence of bottlenose dolphins in Doubtful Sound during 2018. Included are the predictors, distance to the fjord wall (Dist\_wall\_m), the relative abundance of girdled wrasse (Girdled\_wrasse), tarakihi (Tarakihi) and sea perch (Sea\_perch) and the percent change in slope (slope) of the top ranked model and models within two AICc (Akaike Information Criterion with a correction for small sample size) points. Displayed are the degrees of freedom (df), AICc points, change in AICc points ( $\Delta$ AICc), model weight, adjusted  $R^2$  (Adj  $R^2$ ) and percent deviance explained (% d.e.).

Rank	Model predictors	df	AICc	$\Delta$ AICc	Model weight	Adj $R^2$	d.e. (%)
1	Dist_wall_m + Girdled_wrasse + Tarakihi	6	85.3	0	0.151	0.390	39.1
2	Dist_wall_m + Girdled_wrasse + Tarakihi + Sea_perch	7	85.6	0.32	0.128	0.405	41.0
3	Dist_wall_m + Girdled_wrasse + Sea_perch	6	86.0	0.73	0.105	0.386	38.6
4	Dist_wall_m + Girdled_wrasse	5	86.5	1.17	0.084	0.361	36.2
5	Dist_wall_m + Girdled_wrasse + Tarakihi + Slope	7	87	1.97	0.056	0.383	39.6

**Table 4.6.** Statistics for predictor variables included in logistic regression models on presence of bottlenose dolphins in Doubtful Sound during 2018. Predictors were present in models that were within two Akaike Information Criterion points of the top model and include: distance from the fjord wall (Dist\_Wall\_m); relative abundance of girdled wrasse (Girdled\_wrasse), tarakihi (Tarakihi) and sea perch (Sea\_perch) and slope of the seabed (Slope).

Predictor	Estimated degrees of freedom	Test statistic ( $\chi^2$ )	p-value	Relative variable Importance
Dist_wall_m	3.142	8.139	0.08075	1
Girdled_wrasse	1	6.791	0.00916	1
Tarakihi	1	3.172	0.07492	0.73
Sea_perch	1	1.819	0.1774	0.47
Slope	1	0.259	0.6109	0.10

Modelling the smoothed response against the predictor variables for the top ranked biotic model provides valuable insights into the relationship dolphins have with potential prey in Doubtful Sound. The probability of finding bottlenose dolphins during 2018 was highest approximately 200m from the fjord wall (Figure 4.7a), at a high relative abundance of girdled wrasse (Figure 4.7b), and a low abundance of tarakihi (Figure 4.7c). Note the relationships are less certain at large distances to the wall and higher fish abundances, observed with an associated increase in the 95% confidence band.



**Figure 4.7.** Effect of explanatory variables from the top ranked logistic generalised additive model, using both abiotic and biotic predictors, on presence of bottlenose dolphins in Doubtful Sound during 2018. The 95% confidence interval of the response is represented by the shaded area. The y-axes show the smooth function of each variable, with the estimated degrees of freedom. (a) distance to the nearest fjord wall (Dist\_wall\_m), (b) the relative abundance of girdled wrasse, and (c) the relative abundance of tarakihi.

Deviance explained increased by approximately 20% in models containing both biotic and abiotic predictor variables, when compared to models containing only abiotic variables (Table 4.7). When biotic variables were added to the model, AICc values decreased by nearly 50 points.

**Table 4.7.** Comparison of abiotic only and biotic/abiotic logistic regression models on presence of bottlenose dolphins in Doubtful Sound during 2018. Displayed are the Akaike Information Criterion values, corrected for small sample size (AICc), the adjusted  $R^2$  and the percent deviance explained (d.e. %).

Data used	Model Predictors	AICc	Adj $R^2$	d.e. (%)
2018 biotic and abiotic	Dist_wall_m + Girdled wrasse + Tarakihi	88.5	0.390	39.1
2018 abiotic only	Dist_Ent_km + Dist_wall_m + Slope	136.62	0.198	19.8

#### 4.4 Discussion

I used GAMs to investigate the role of biotic variables on habitat use of bottlenose dolphins in 2018. The performance of the best model containing only abiotic variables was compared with the best model containing both abiotic and biotic variables. In terms of deviance explained, model performance improved by nearly 20% with the inclusion of biotic variables. When potential prey were added to the model, girdled wrasse was the only significant predictor variable and was one of the most important. The relative abundance of girdled wrasse was positively associated with the probability of sighting bottlenose dolphins, while abundance of tarakihi had a negative relationship.

A positive relationship with potential prey species is expected for predators. In Doubtful Sound, dolphins appear to favour areas with a high abundance of girdled wrasse. This strong positive relationship suggests that girdled wrasse may be an important food source within the fjords, while the negative relationship for tarakihi suggests the opposite. Girdled wrasse have been described as generalists that can exploit habitat from the inner to the outer fjord (Davis and Wing 2012); a pattern which is similar to the dolphins' own habitat use (see Ch. 2). Because it is unlikely that the dolphins are specialists on only one prey species or area, it is logical that their habitat use would reflect that of a more generalist prey. It is interesting, however, that girdled wrasse was a more influential predictor than diversity (Appendix 13). Greater diversity in an area would suggest a more complex food web (Paine 1966; Pimm et al. 1991), which can bring greater stability and resilience (e.g. Chapin et al. 2000). If girdled wrasse abundance is

related to diversity, as is suggested by the correlation between these two predictors, there is potential that the dolphins are also targeting areas of higher diversity, that are inherently more resilient to environmental change. This may help explain the stability in dolphin habitat use over time (see Ch. 2).

This study was the first to incorporate data on abundance of potential prey into analyses of dolphin habitat use in Doubtful Sound, and shows that prey more strongly influence where dolphins go than the abiotic characteristics of the environment. This is not unexpected, and has been shown in other systems (e.g. endangered butterflies and songbirds Preston et al. 2008; terrestrial mammals and mosquitoes, González-Salazar et al. 2013; and, cerrado parrots, de Araújo et al. 2014). For dolphins, however, demonstrating the link between distribution and prey has not been straightforward. Torres et al. (2008) found no improvement to model performance when prey parameters were added. While other studies have shown an association between dolphin habitat use and their prey, this has not been directly compared to abiotic predictors (e.g. Heithaus and Dill 2002; Benoit-Bird et al. 2004; Certain et al. 2011).

The results of this study may help in managing the populations of bottlenose dolphins in Fiordland. The relative abundance of fish has been demonstrated to be an important correlate, if not driver, of habitat use by the dolphins. I argue that this result suggests multispecies approaches to management, in addition to being more ecologically sound than single species approaches, could be more appropriate. The current spatial management in Doubtful Sound focusses on reducing boat pressure in areas intensively used by dolphins. This is a reasonable strategy, but it does not include a multispecies approach, or incorporates *why* dolphins have high-use areas. This study found that dolphins target areas with high abundance of girdled wrasse, a variable which may be representative of diversity. Although girdled wrasse themselves are not targeted by fishing activities, fishing within the areas that they inhabit would act to reduce diversity and degrade the habitat (McClanahan and Shafir 1990; Wilson et al. 2008, 2010). Overlap between fishing within the fjord and the core habitat of the dolphins could undermine current protection. Extending protection to reef associated fish, through fisheries limits or marine protected areas in important dolphin habitat, may confer additional benefits to the dolphins.

Although the Doubtful Sound population was the focus of this study, these results may be relevant to the population of bottlenose dolphins in Dusky Sound. If fish are an important driver of habitat use in Doubtful Sound, it is reasonable that they will also be important for the

dolphins in Dusky Sound. The distribution, abundance and diversity of fish may explain why there are similar patterns in dolphin habitat use between these two populations. A potential way to extrapolate these results to the population in Dusky Sound would be to predict the distribution of reef fish through fish focussed GAMs. Appropriating results to other systems should be done cautiously, however, as important processes may vary, or be occurring on a different scale (Englund and Cooper 2003). Such models would need to be validated with independent data on prey in Dusky Sound.

All studies have limitations and it is important to identify how the methods may be improved or how this research can be expanded in future studies. The use of BUV was a practical supplement to dolphin surveys and provided an effective method for sampling reef-associated fish (Willis and Babcock 2000; Roberts et al. 2005; Miller et al. 2005; Jones et al. 2015). BUVs however, have limited ability to sample herbivorous, epipelagic or pelagic fish, which may be important in the diet of these dolphins (e.g. Colton and Swearer 2010). Not all fish come to bait and the benthic, vertical position of the BUVs will reduce the chance of observing epipelagic and pelagic fish. In addition to this, deeper water species will also be underrepresented in this analysis. Species such as telescope fish, sprat, mackerel, squid, red cod and rattails were not sampled in this study and may form an important part of the dolphins' diet (Schneider 1999; Lusseau & Wing 2006). Combining a range of methods to sample the various fish species would be an improvement in comparing the distribution of potential prey to dolphin distribution. Furthermore, fish size, not just abundance, is also likely to be important. The BUV system in this study used a single camera only, so measurements could be made only if the fish was level with and close to the scale bar. Using a stereo BUV system to gain accurate size estimates would be an improvement for future studies as would incorporating other methods to sample a wider diversity of fish species (Colton and Swearer 2010; Langlois et al. 2010).

Even though model performance was dramatically improved, approximately 60% of the deviance in the dolphins' habitat use remained unexplained. This may be due to the coarse resolution of the data and/or because important factors were not measured. For example, sociality within dolphin groups is likely to be an important factor in where individuals choose to go. The dolphins of Doubtful Sound feature long-lasting, strong, social bonds which are likely to be important for information transfer and finding food (Lusseau et al. 2003; Johnston et al. 2017). Human activities could be another important predictor. Boat-based tourism directly influences the behaviour of the dolphins (Lusseau 2003a, b; Lusseau and Higham 2004; Guerra et al. 2014), but this has not yet been formally incorporated into studies of habitat use. Building

these factors into future models and using finer-scale abiotic predictors (as described in chapter three), should further improve model performance.

This study provided insights into the relative importance of potential prey in determining where the dolphins choose to go within the fjord. Prey abundance appears to be a major driver of habitat use and these findings support previous research on the type of prey that is important for the dolphins. Therefore, if management is to be effective long-term for this endangered population, protecting prey species will be a valuable addition. Ensuring that reef fish are protected from human activities in areas of high use by the dolphins could encourage food web stability and the dolphins' continued use of this habitat.



## Chapter 5

### General Discussion

Understanding how animals use their habitat is central to understanding their ecology and behaviour. Additionally, knowledge of habitat use is invaluable for making recommendations on management options. This is because if we know where individuals go, we know which areas to protect, regardless of what the human impacts are. In this thesis I asked three questions concerning the bottlenose dolphins of Doubtful and Dusky Sounds: 1) What is the current and long term distribution of the dolphins; 2) What are the abiotic drivers of habitat use; and 3) How do biotic factors influence habitat use? Although habitat use has been investigated previously, this study provided new perspectives via analysis of a much longer-term dataset and, for the first time, incorporates data on abundance of potential prey. To reduce impacts of tour boats on the dolphins (Lusseau 2003a, b; Lusseau and Higham 2004; Guerra et al. 2014), spatial management has been implemented in Doubtful Sound since 2008 (Department of Conservation 2008). My research has demonstrated consistent use of core areas by the bottlenose dolphins through time, validating an area-based approach to threat reduction, as well as the importance of potential prey. These findings contribute to our understanding of the ecology of Fiordland bottlenose dolphins and how they use the environment.

#### **5.1 Summary of results**

This thesis focussed on the habitat use of bottlenose dolphins in Fiordland. In chapter two, I quantified the distribution of the dolphins within their respective fjord environments, identifying core habitats that were consistent over time. Seasonal variation in habitat use is a key pattern in these fjord systems (Schneider 1999; Henderson 2013; Ch 2). This is most obvious in Doubtful Sound, where one summertime high-use area (within Crooked Arm) is very rarely used in winter. A similar pattern holds in Dusky Sound; despite the same general areas being used year-round, habitat use shifted from closer to the inner fjord in summer, to closer to the outer fjord in winter. Seasonal variation in habitat use was more pronounced for the dolphins in Doubtful Sound, possibly because Doubtful Sound has greater seasonal

fluctuations in SST than Dusky Sound (Henderson 2013). When temperature data were collected on a fine scale the correlation between distribution and SST was observed in both fjords (Henderson 2013). That these two separate populations show similarities in habitat use suggests that similar processes are driving these patterns within the fjords.

In studies of marine mammals we frequently have detailed information on where individuals go, but we seldom know why. Investigating the drivers of habitat use was completed using species distribution models (SDMs; Ch. 3 & 4). In chapter three, I used the long-term dataset to relate abiotic variables to occurrence data on the bottlenose dolphins in both Doubtful and Dusky Sounds. Although I was able to identify some useful predictors of habitat use, these models showed that abiotic factors alone are insufficient to explain the variation in dolphin occurrence. Therefore, in chapter four I investigated the role of biotic factors, specifically the availability of potential prey. I used similar methods to those in chapter three, but focussed only on data collected during 2018, a year in which I had deployed baited underwater video systems to collect data on relative abundance of fish, while dolphins surveys were conducted simultaneously. Addition of prey data into the SDMs improved their performance dramatically. This result, while expected, is significant for several reasons. First, this study is one of very few that has quantified prey and incorporated those data into analyses of dolphin habitat use (e.g. Heithaus and Dill 2006; Torres et al. 2008). Secondly, the method chosen was entirely non-invasive (to the dolphins and the prey) yet managed to produce data that proved not just useful but important. Thirdly, demonstration that prey were an important driver of dolphin distribution illustrates that management of dolphins needs to be more ecologically focussed; it needs to incorporate potential impacts on fish species.

## **5.2 Management implications**

Like all marine mammals in New Zealand waters, the bottlenose dolphins of Fiordland are protected from disturbance by boat activity under the Marine Mammal Protection Act (1978; 1992). This limits the number of vessels that can be nearby, indicates how they should approach, and sets speed limits near the animals. Pressure from tourism highlighted by Lusseau and Higham (2004) has led to additional protection for the resident population of dolphins in Doubtful Sound in the form of a voluntary Code of Management (COM). This COM has two main goals: to ensure that encounters between vessels and dolphins are on the dolphins' terms, and to limit chance encounters through Dolphin Protection Zones (DPZs). The two other Fiordland populations of bottlenose dolphins have not had such protection. The northern

Fiordland population of dolphins is not resident, and the Dusky Sound population has not experienced the same levels of tourism pressure.

Protecting species that are targeted for commercial or recreational purposes is necessary to ensure that they are not negatively impacted by anthropogenic activities. Ideally, such management allows the integrity of the ecosystem to be preserved, including complex food webs and the services that they provide (Chapin et al. 2000). It also can allow the activity, which may have economic and social benefits, to continue sustainably. In Fiordland, the dolphins are an integral part of the ecosystem. Although the boat-based tourism industry does not exist to watch dolphins, they are clearly part of the attraction. There is high traffic of tour vessels in Doubtful Sound, if all aim to watch the dolphins the risks posed may be significant. Because this is a small population, the same individuals will be affected repeatedly and the effects are likely to accumulate over time (Lusseau 2003a, b; Guerra et al. 2014). Effects of tourism in Fiordland have been thoroughly described previously (Lusseau 2003a, b; Lusseau and Higham 2004; Guerra et al. 2014), so in this thesis I did not attempt to review those impacts. Instead I aimed to evaluate the current spatial management, because if the core habitat is protected, impacts will be reduced. I also aimed to provide recommendations for future spatial management of the bottlenose dolphins in both Doubtful Sound, and Dusky Sound.

### 5.2.1 Risk assessment

In Doubtful Sound in 2002, a decline in abundance of bottlenose dolphins was observed (Currey et al. 2007) which was attributed to a dramatic reduction in calf survival (Currey et al. 2009a). The drivers of this decline are unknown, and the population has been slowly increasing since. However, this highlights the risk to small populations of sudden changes in the environment (Courchamp et al. 1999). Furthermore, although the dolphins have shown consistency in habitat use within the fjord, there have been important changes over time. The most obvious of these is that the once resident dolphins are now frequently leaving Doubtful Sound for significant periods of time (Henderson et al. 2013). Under IUCN criteria for regional assessment, the bottlenose dolphins of Doubtful Sound are considered Critically Endangered (Currey et al. 2009b). The above observations confirm the fragility of this population, and the necessity for effective management.

The risk to dolphins in Dusky Sound is less severe. The dolphins have a larger population size and reside in a fjord where there is lower tourism pressure. There is no anthropogenic input of fresh water via a hydro-electric tailrace, and other anthropogenic influences, such as tourism,

are thought to be less. However, while there is no evidence of broad-scale changes or past declines, there is a much shorter dataset from which to detect change. Furthermore, anecdotal reports suggest tourism and boat use in Dusky Sound have been increasing. Although implementing management in Dusky Sound is not as urgent as in Doubtful Sound, it may safeguard the dolphin population if anthropogenic activities continue to increase. Knowing where MPAs would be best situated (Ch. 2) removes one of the impediments to effective management and will help conservation decisions to be made quickly.

### 5.2.2 Current management of Doubtful Sound

My results from chapter two provided the ability to review the placement and effectiveness of DPZs in Doubtful Sound. Although some of the DPZs are located in areas that were frequently used by the dolphins (e.g. Crooked Arm and Bradshaw Sound) in total there is less than 20% overlap with core dolphin habitat (Figures 2.15; 2.16). This indicates that chance encounters with vessels are still likely to occur over a large portion of important dolphin habitat. Seasonal variation in habitat use also influences the effectiveness of DPZs as the dolphins use the inner fjord more during summer but shift during winter to the outer fjord, where there is no DPZs.

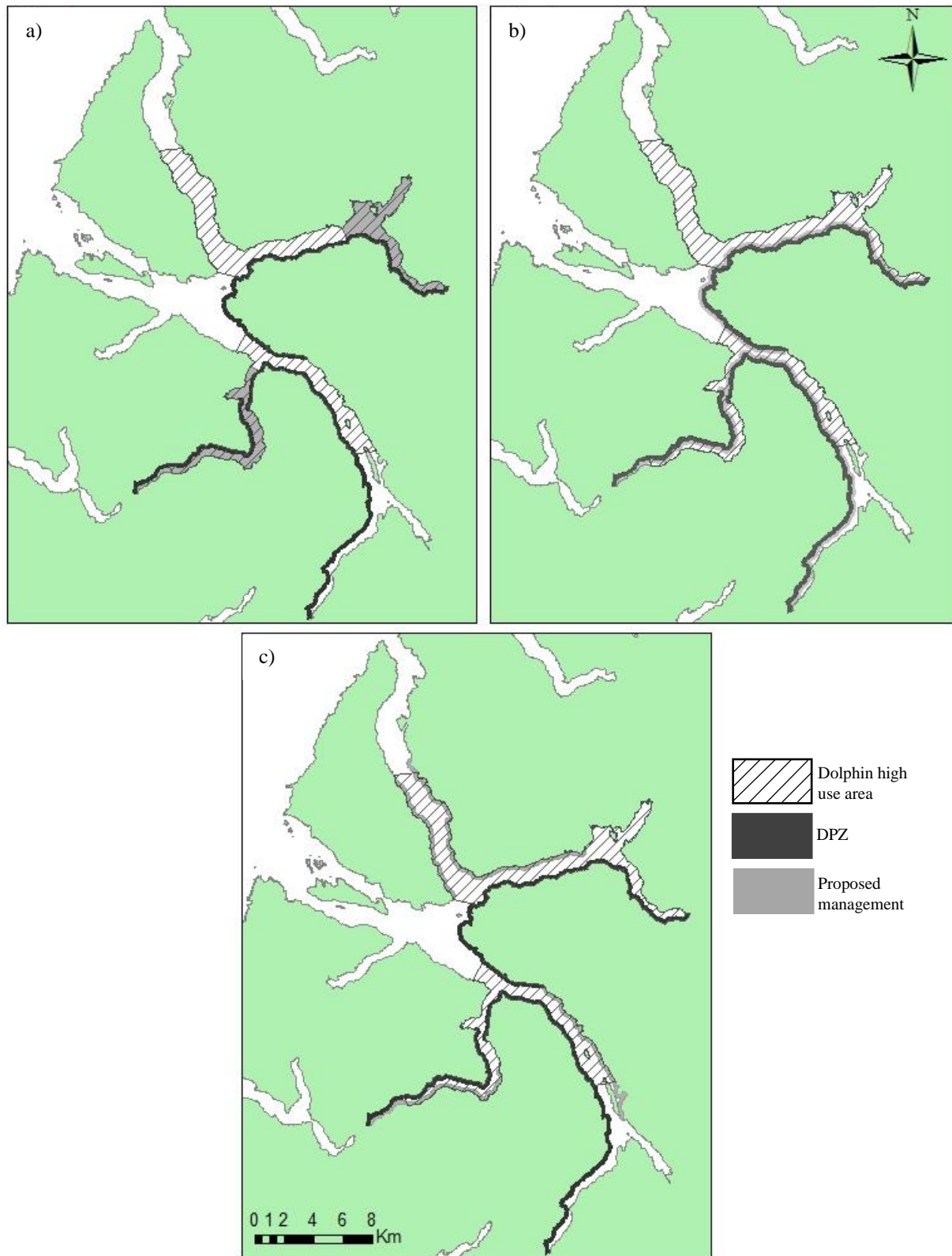
The rules to reduce vessel encounters with the dolphins in Doubtful Sound are voluntary. Tour operators, who generally comply with the COM (Guerra and Dawson 2016), are not the only users of the fjord. Other commercial operators and recreational fishers use the fjord and commonly travel at speed through DPZs. While they are encouraged to comply with the COM, they often do not. This means that the efforts made by the tourism companies to reduce chance encounters with the dolphins may be undermined by other fjord users. While not part of the COM, the amount of time that researchers can spend with dolphin groups is limited by DOC, as is the total amount of time research vessels may spend within DPZs.

### 5.2.3 Future management options

If all boats have the potential to affect dolphin behaviour it is logical that all fjord users are targeted by protection. Therefore, if the efforts of the tourism industry in protecting these endangered populations are not to be undermined, the voluntary aspects of the COM should be made into law and become mandatory

In Doubtful Sound, the DPZs currently cover between 10 and 15% of core dolphin habitat depending on the season (Figure 2.17). Based on the results of this thesis, options to increase the level of protection afforded by DPZs in Doubtful Sound include:

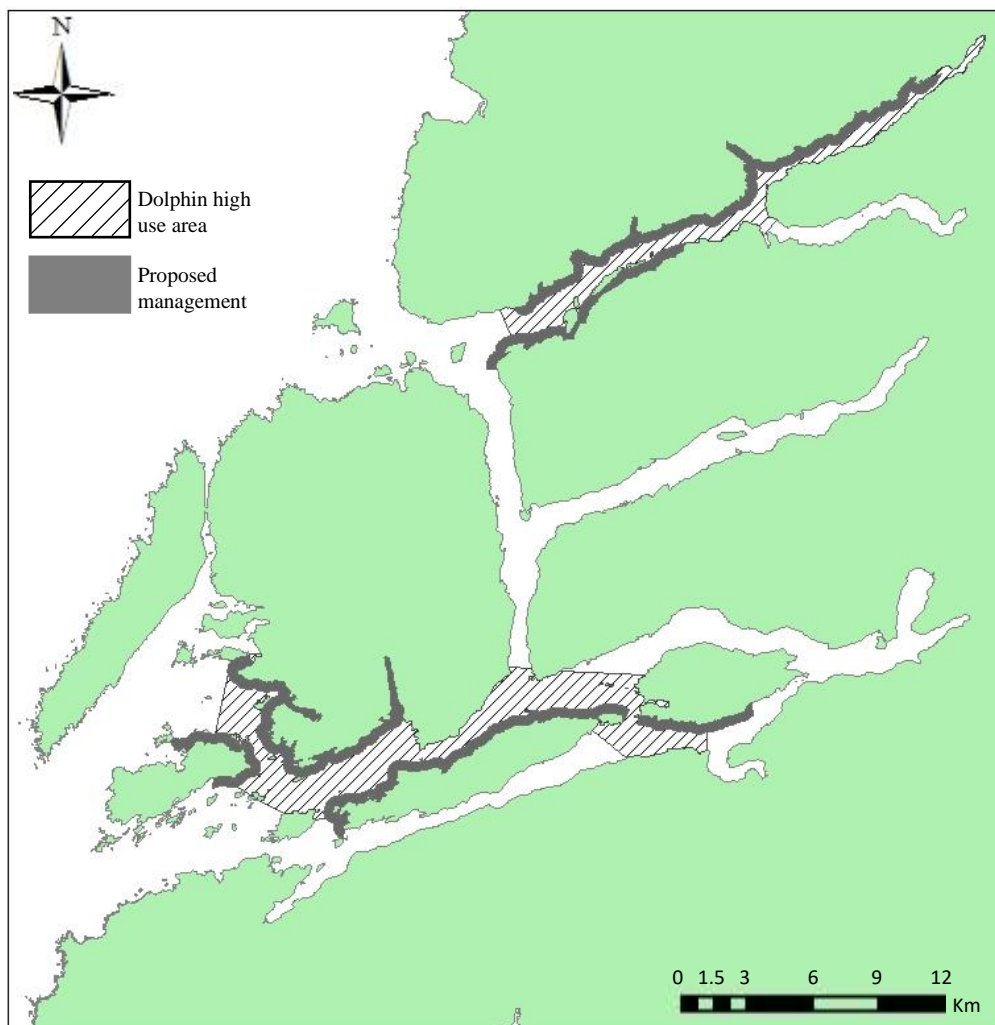
1. Exclude vessels from areas of the fjord demonstrated by KDEs to have the highest dolphin densities, e.g. the northeast end of Bradshaw Sound and Crooked Arm (Figure 5.1a)
2. Increase the width of current DPZs to 400m, based on the response to the “distance to the fjord wall” variable included in the SDMs produced in chapter three (Figure 5.1b).
3. Include additional DPZs in areas of the fjord that are included in dolphin core habitat, e.g. DPZs could be established on both walls in areas such as Crooked Arm and in additional areas, such as Thompson Sound (Figure 5.1c)
4. Set tangible goals for protecting dolphin habitat and adjust protection accordingly. For example DPZs could aim to protect 50% of core dolphin habitat.



**Figure 5.1.** Options for future spatial management of bottlenose dolphins in Doubtful Sound. Areas included in current management, Dolphin Protection Zones (DPZs), are represented in dark grey. Dolphins high-use areas are represented by lines and examples for future management are represented in light grey. Example options presented are: a) closing off high use areas, b) extending the DPZs to 400m, and c) creating and extending DPZs in high use habitat.

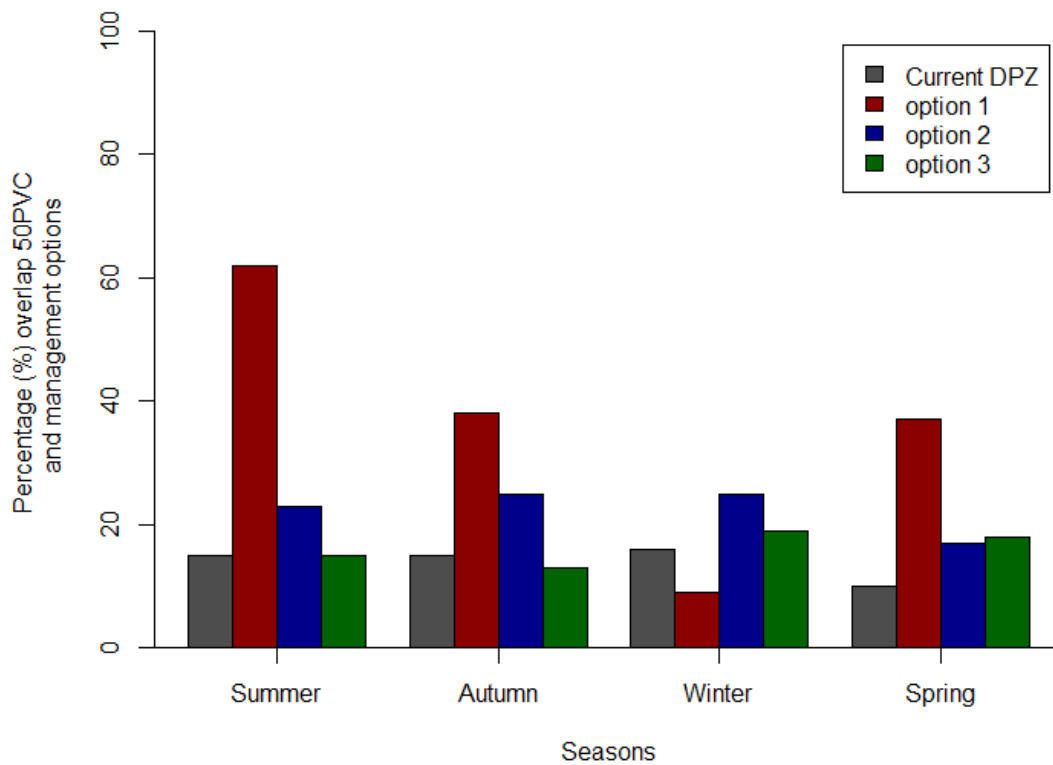
The dolphins of Dusky Sound show similarities in habitat use to those of Doubtful Sound. Although there is no DPZs in Dusky Sound, the consistency in habitat use over time (Ch. 2) suggests that spatial management is well suited to this population as well. Therefore similar approaches to the COM in Doubtful Sound could be applied by defining DPZs in high use areas:

1. The probability of encountering dolphins increases within 400m of the fjord wall (Figure 3.4b), DPZs could therefore extend to this distance (Figure 5.2)
2. Set tangible goals for protecting dolphin habitat and establish MPAs accordingly. For example DPZs could aim to protect 50% of core dolphin habitat.



**Figure 5.2.** Potential options for areas where Dolphin Protection Zones (DPZs) could be established in Dusky Sound. Bottlenose dolphin high use areas are represented by the lined areas and potential DPZs are represented in dark grey.

To assess the effects of these proposed options I calculated the percent overlap with core habitat, as estimated in chapter two. In Doubtful Sound all options would increase protection, though only for options one and two is this increase greater than 20% (Figure 5.3). In Dusky Sound introducing DPZs in the suggested areas would provide protection to 20% of dolphin core habitat. If other protection options are proposed I am willing to work with the Department of Conservation in quantitatively assessing their potential for including core habitat.

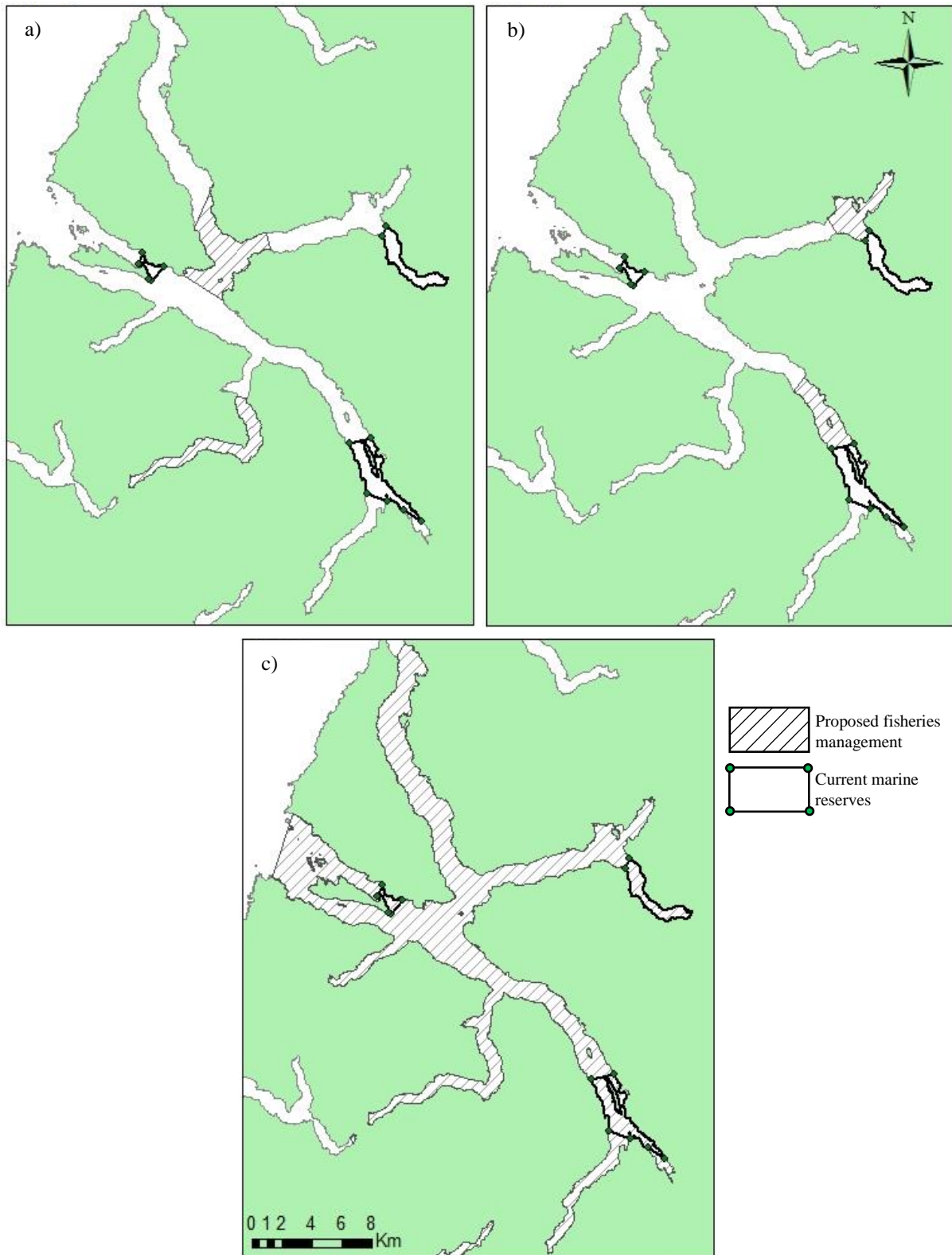


**Figure 5.3.** The percentage overlap between bottlenose dolphin core habitat and potential management options in Doubtful Sound during each season. Current management is represented in dark grey; option 1) is closing off ends of the fjords to all vessel traffic; option 2) is to increase the dolphin protection zones (DPZs) to 400m; and option 3) is to create and extend DPZ.

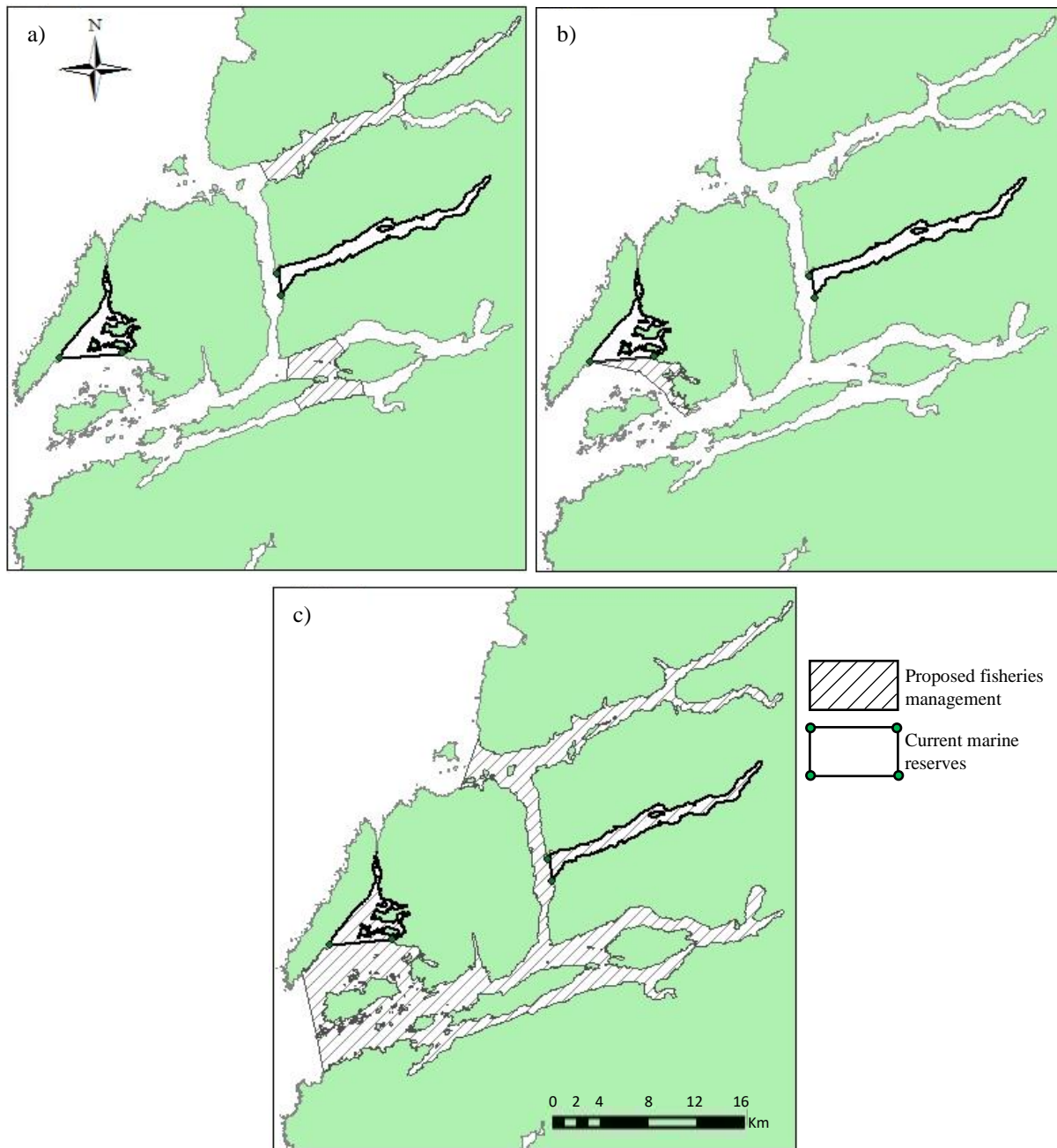


The major finding of this thesis was that the distribution of dolphins within the fjords is affected by the distribution and abundance of their potential prey. This has not been shown previously and suggests that a more ecosystem-based approach to management will be beneficial to the dolphins. Protecting reef fish and their associated habitat is an option for future management in both Doubtful and Dusky Sounds. This could be achieved by:

1. Restrict or prohibit fishing of reef fish in areas of the fjord demonstrated by KDEs to have high dolphin densities. In Doubtful Sound these areas include Crooked Arm and the junction between all the Sounds (Figure 5.4a) and, in Dusky Sound, in Breaksea Sound and the Bowen Channel (Figure 5.5a).
2. Current marine reserves could be extended, so that the boundaries cover a greater portion of dolphin core habitat (Figure 5.4b; 5.5b). The Gaer Arm marine reserve in Bradshaw Sound and the Five Fingers marine reserve in Dusky Sound are good candidates, as they are close to high use areas.
3. Prohibiting fishing within the fjord limits of both Doubtful and Dusky Sound (Figure 5.4c; 5.5c)



**Figure 5.4.** Options for future ecosystem-based management for potential prey of bottlenose dolphins in Doubtful Sound. Current marine reserve areas are represented with black lines, examples for future management are represented by the lines. Example options presented are: a) targeted protection of prey within high use dolphin habitat, b) extending current marine reserves, and c) closing off entire fjord to fishing.



**Figure 5.5.** Options for future ecosystem-based management for potential prey of bottlenose dolphins in Dusky Sound. Current marine reserve areas are represented with black lines, examples for future management are represented by the lines. Example options presented are: a) targeted protection of prey within high use dolphin habitat, b) extending current marine reserves, and c) closing off entire fjord to fishing.

### 5.3 Future Directions

The Fiordland bottlenose dolphin project began in 1990 and in 2007 was extended to include long-term monitoring in Dusky Sound. The value of long-term datasets such as these cannot be overstated. They enable the ability to follow population parameters through time for management purposes (e.g. Russ and Alcala 2004; Wilson et al. 2004; Gormley et al. 2012), and allow robust estimation of crucial demographic parameters such as adult survival rate, which for long-lived animals cannot be reliably estimated from a short time series. In addition, long-term studies of small populations are vital for understanding processes that contribute to extinction (e.g. demographic stochasticity, reproductive heterogeneity; anthropogenic pressures; Bejder et al. 2006; Currey et al. 2007; Brough et al. 2016). While these populations have been extensively studied, a range of important questions remain. I focused specifically on the habitat use of bottlenose dolphins in Fiordland and as such have identified knowledge gaps that are directly relevant to this.

#### 1) Regarding future habitat use studies:

Prior to this thesis, the extent of our knowledge on diet of bottlenose dolphins in Fiordland comes from one study by Lusseau and Wing (2006) on the dolphins in Doubtful Sound. Increasing our understanding of what resources the dolphins are using will enable more effective management. New techniques are available for dietary analyses and collection of biotic variables. Therefore I recommend:

- a) Dietary analyses using new approaches in DNA sequencing of faeces (e.g. Ford et al. 2016), for both populations in Doubtful and Dusky Sound.
- b) Concurrent distribution analyses of the dolphins and pelagic fish. If sonar techniques were used throughout the fjord, the relationship between pelagic fish and dolphins could be measured in real time. (e.g. Benoit-Bird et al. 2004; Benoit-Bird et al. 2013; Lawrence et al. 2016; Brough et al. 2019).
- c) Investigation of deep-water fish and their relevance to bottlenose dolphins in both the diet and for distribution analyses.

There are similarities between the dolphins in Doubtful and Dusky Sounds, however, there are also clear differences. Therefore, I recommend:

- d) To investigate biotic influences on the distribution of bottlenose dolphins in Dusky Sound.

## 2) Future direction for the long-term dataset

The long-term information gathered during the Fiordland bottlenose dolphin project is extremely valuable, and has significant potential for further analysis, including:

- a) Creation of individual-based population models that would incorporate individual-specific data (e.g. reproductive histories) to more adequately model population trends and extinction probability.
- b) The continuation of the long-term monitoring programmes in Doubtful and Dusky Sound is important as these populations remain at risk. It is also necessary to ensure that management remains effective. The long term monitoring project should be expanded to include distribution analyses.
- c) Management decisions could be evaluated quickly and efficiently by using the wealth of existing data and focussed questions to guide future monitoring. This would enable an adaptive-management approach to be taken.

## 5.4 Concluding remarks

This research solidifies and expands our knowledge on a key ecological aspect of endangered populations of bottlenose dolphins in Fiordland. It demonstrates the importance of prey abundance to habitat use by dolphins. This study shows that dolphin habitat use has been stable over many years, endorsing the DPZ concept of managing impacts spatially. However, it also shows very limited overlap between core dolphin habitat and the current DPZ areas. The stability of core areas contrasts with an increasing trend for the Doubtful Sound dolphins to venture beyond the fiord. Such excursions do not register in my spatial analysis because areas outside the fiords were not sampled, but they appear to indicate change and may be important.

This study has demonstrated the value of habitat-use studies, including the use of kernel density estimation and multi-model inference to elucidate factors influencing habitat use. These methods enabled me to identify core habitat for bottlenose dolphins and the factors that drive its preferential use, thus revealing ecological insights important for guiding management decisions. This will help to preserve the integrity of the areas within the fjords which are important to the dolphins, and, hopefully, the key role of the dolphins as top predators in these ecosystems. This research would not have been possible without the long-term dataset; the value of collecting data on these long-lived animals over many years cannot be overstated.



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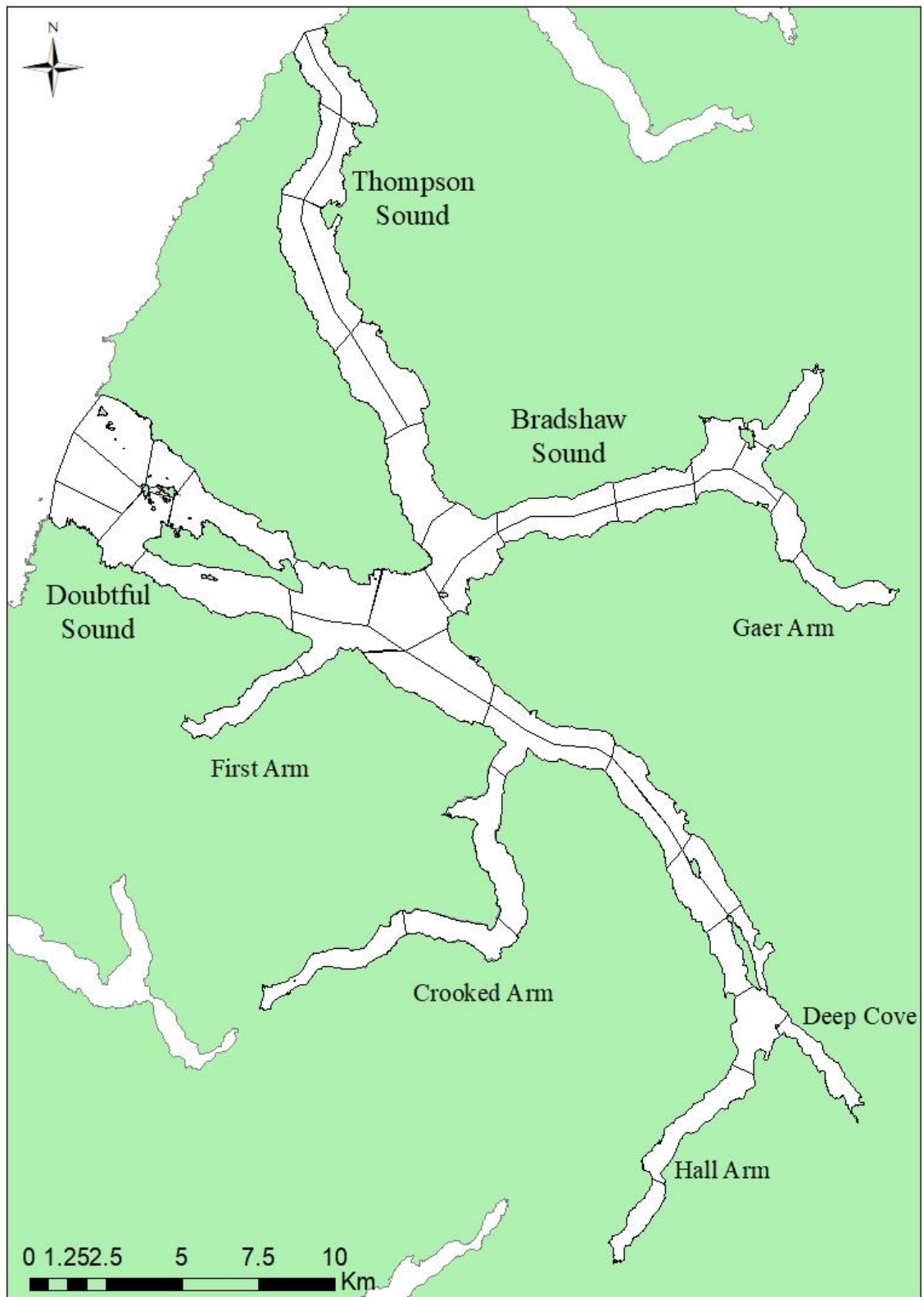
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## Appendices

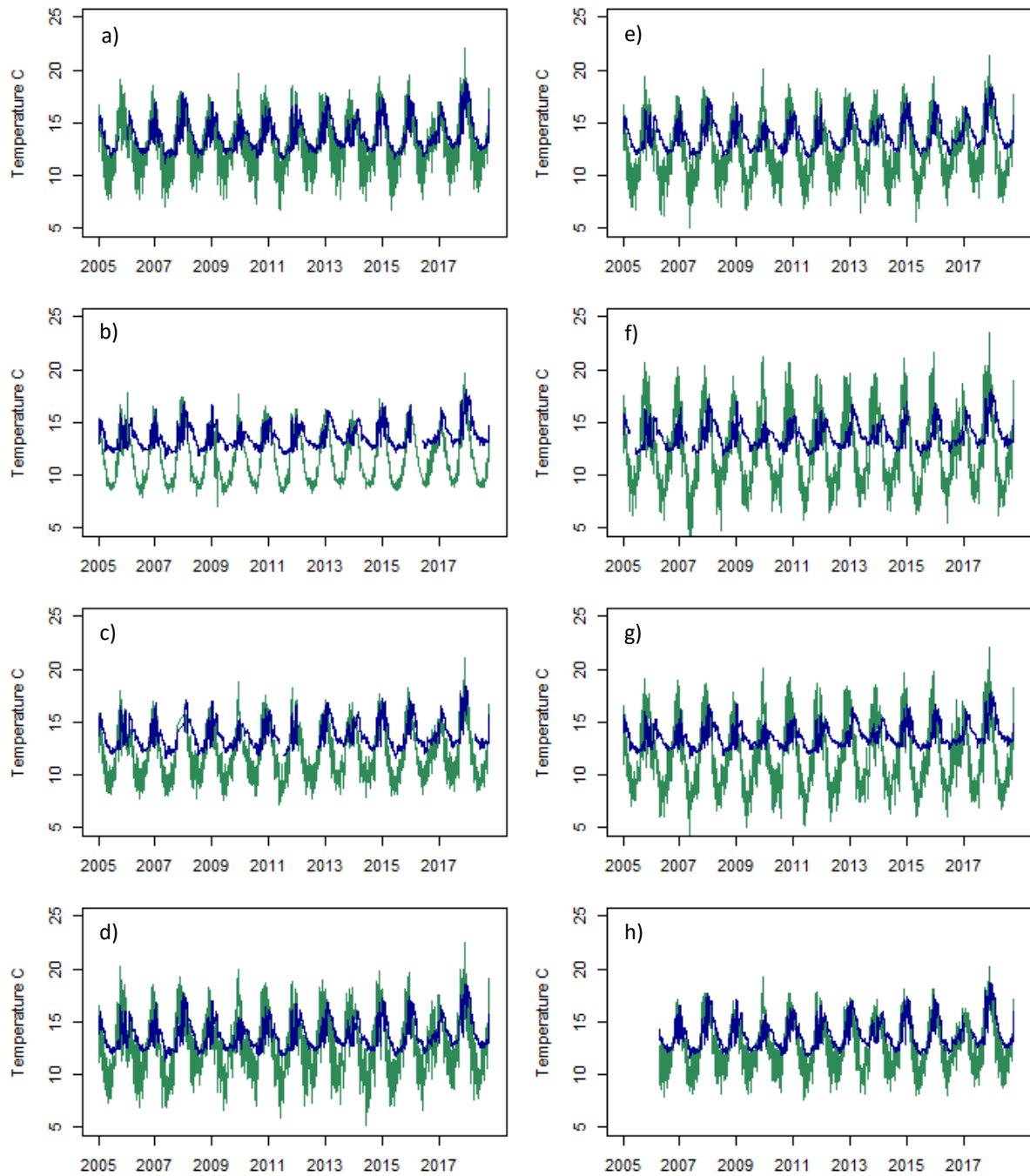


**Appendix 1.** Zones within Doubtful Sound that were considered for survey effort (denoted by a black line), each time a survey route intersected a zone it was considered surveyed for bottlenose dolphin presence.

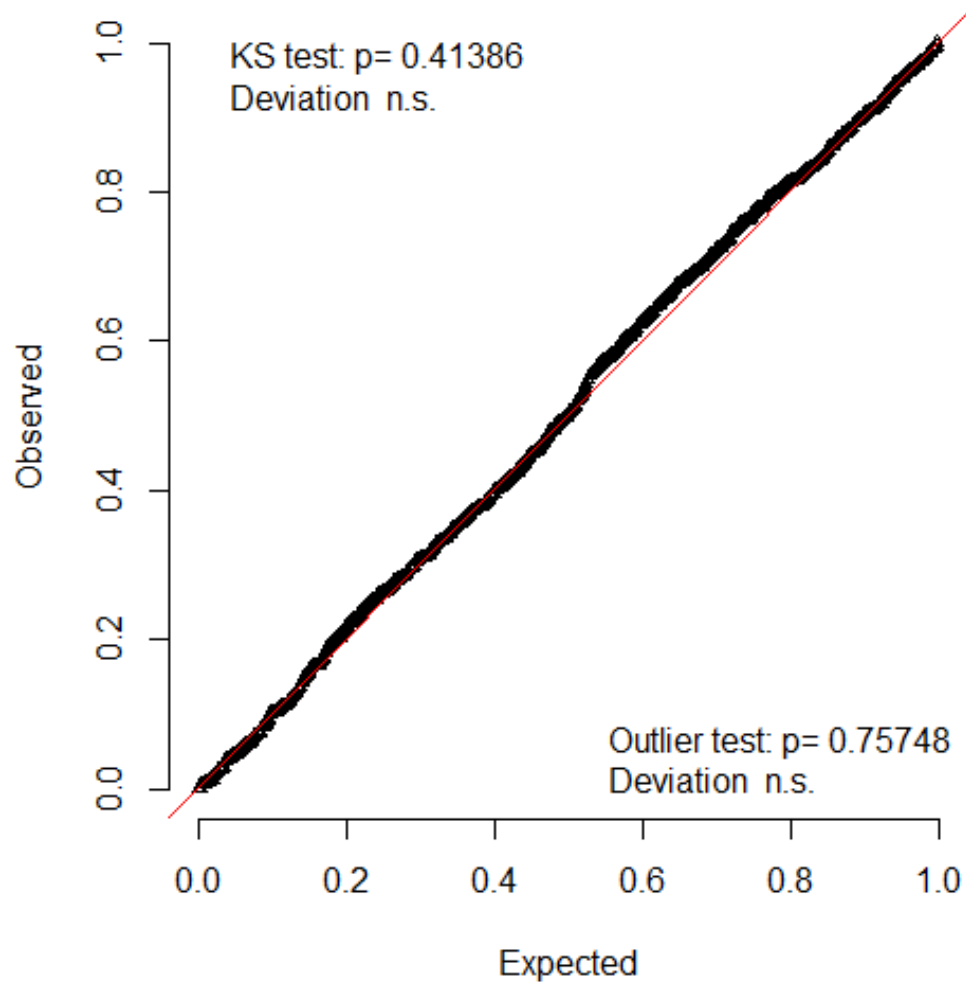


**Appendix 2.** Areas within Dusky Sound that were considered for survey effort (denoted by a black line), each time a survey route intersected a zone it was considered surveyed for bottlenose dolphin presence.

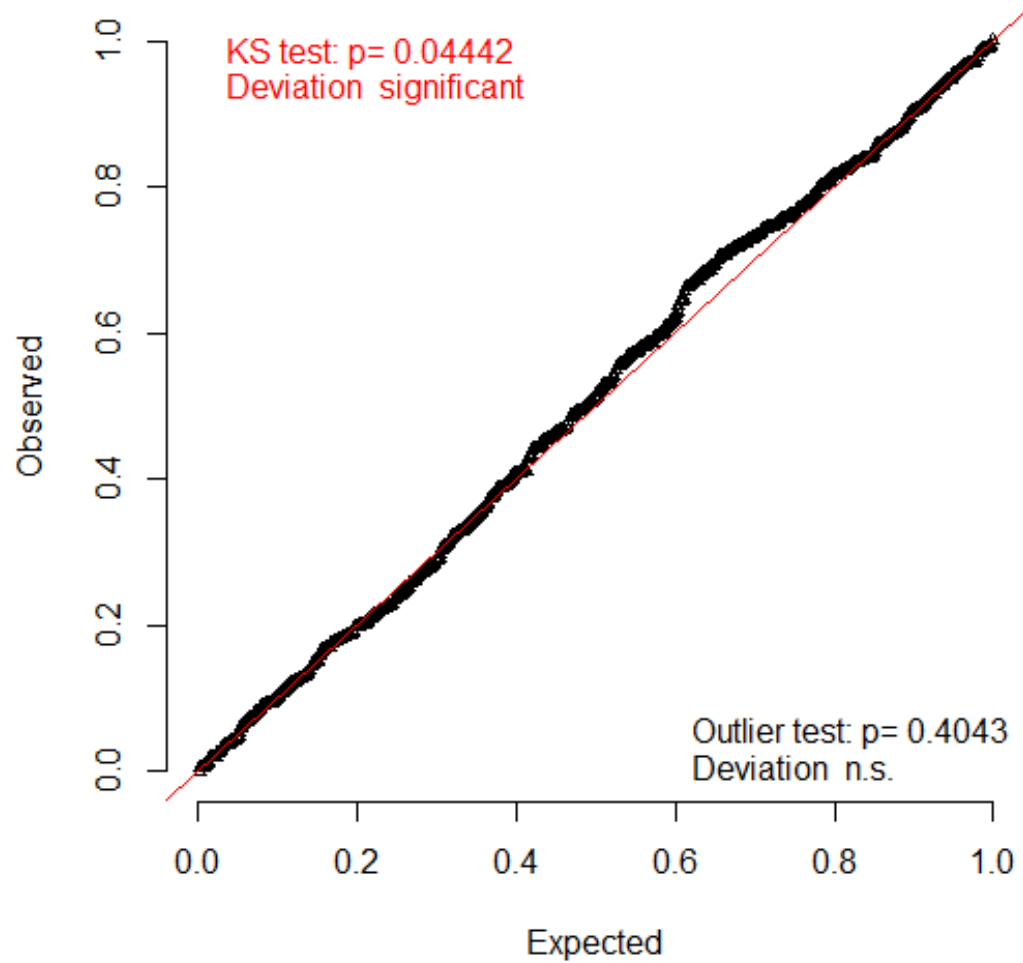




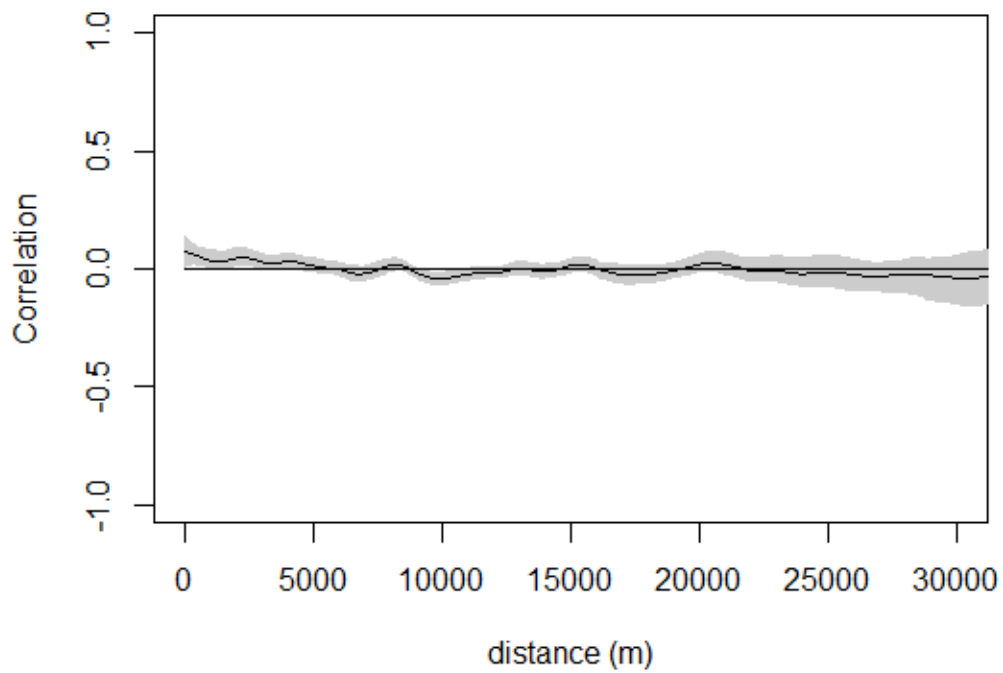
**Appendix 3.** Time series of mean daily temperatures at: 0.5m (green line) and 19m depth (blue line), from 2005 to 2018, at eight oceanographic monitoring buoys around Doubtful Sound: a) Thompson Sound b) Deep Cove c) Main Channel in Doubtful Sound d) Bradshaw Sound e) First Arm f) Crooked Arm g) Hall Arm h) Bauza Island.



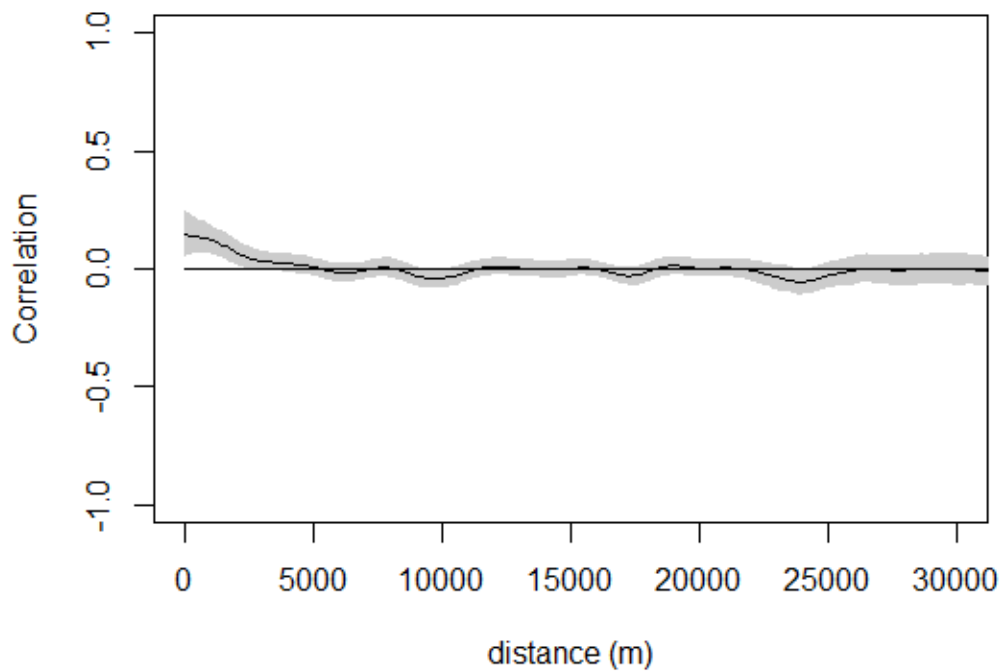
**Appendix 4.** Logistic regression quantile-quantile plot of simulated model residuals (x-axis) against observed model residuals (y-axis) for the best fitting habitat model for bottlenose dolphins in Doubtful Sound. Data was collected between 2005 and 2018.



**Appendix 5.** Logistic regression quantile-quantile plot of simulated model residuals (x-axis) against observed model residuals (y-axis) for the best fitting habitat model for bottlenose dolphins in Dusky Sound. Data was collected between 2009 and 2018.



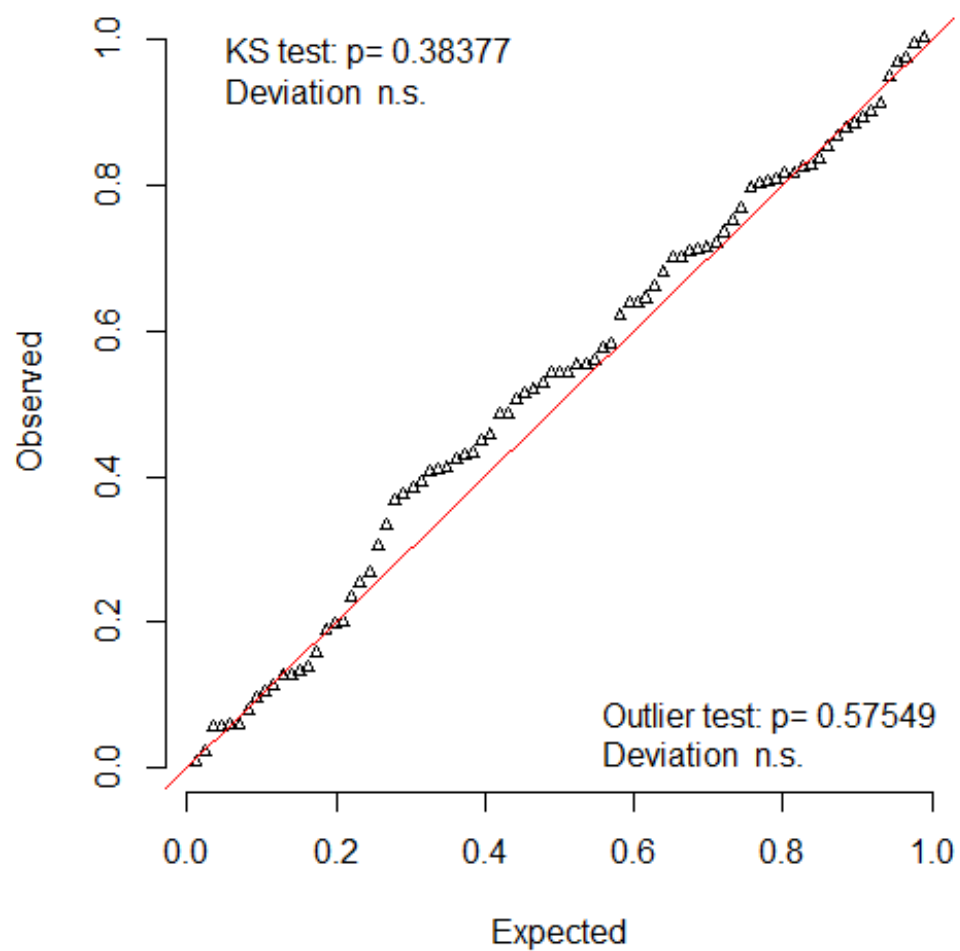
**Appendix 6.** Correlogram of residuals for the top regression habitat model for bottlenose dolphins in Doubtful Sound. Shows the correlation between residuals at different distances. The shaded area represents the 95% pointwise bootstrap confidence interval.



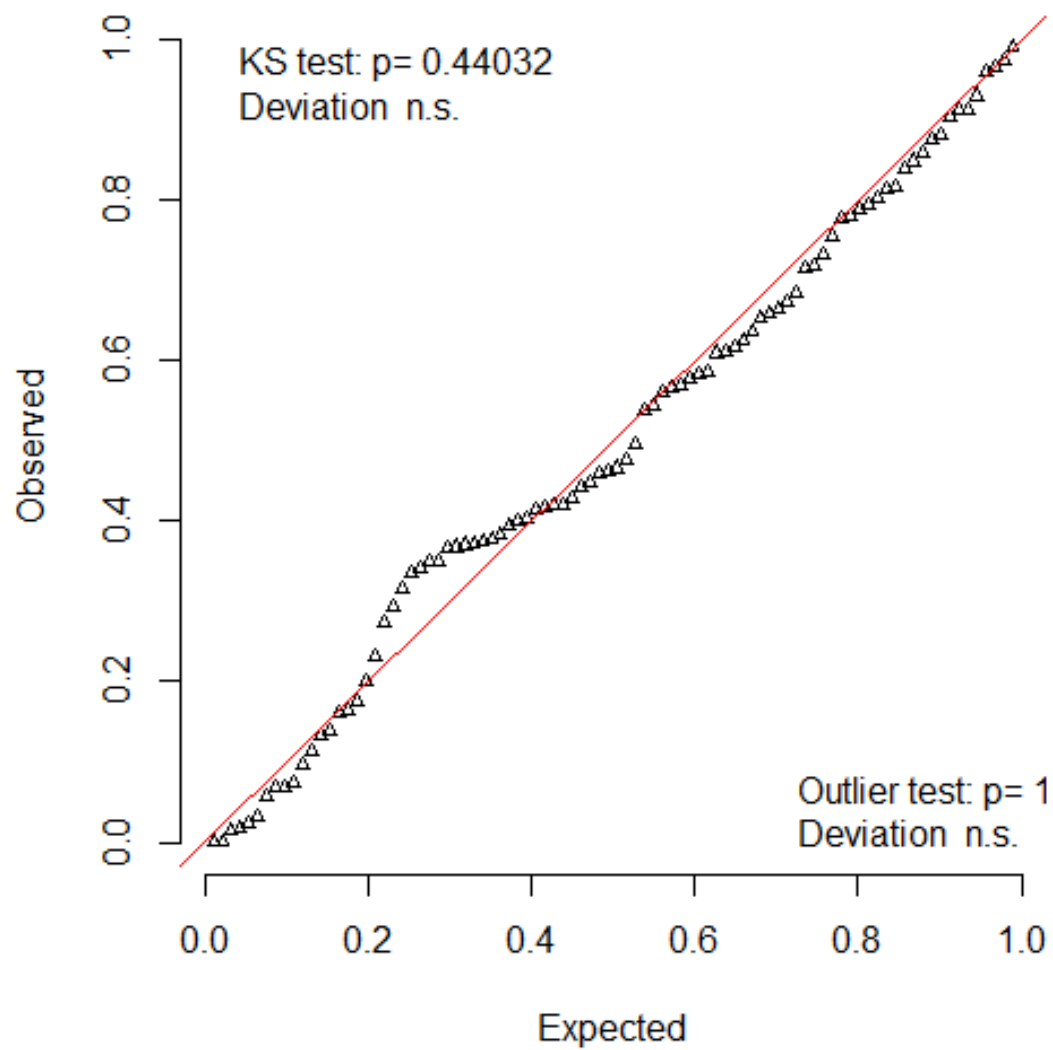
**Appendix 7.** Correlogram of residuals for the top regression habitat model for bottlenose dolphins in Dusky Sound. Shows the correlation between residuals at different distances. The shaded area represents the 95% pointwise bootstrap confidence interval.

**Appendix 8.** Univariate model results used in model selection between concurred predictor variables. In Doubtful Sound depth was concurred with both distance to the wall and slope, while in Dusky Sound depth and distance to the wall were concurred.

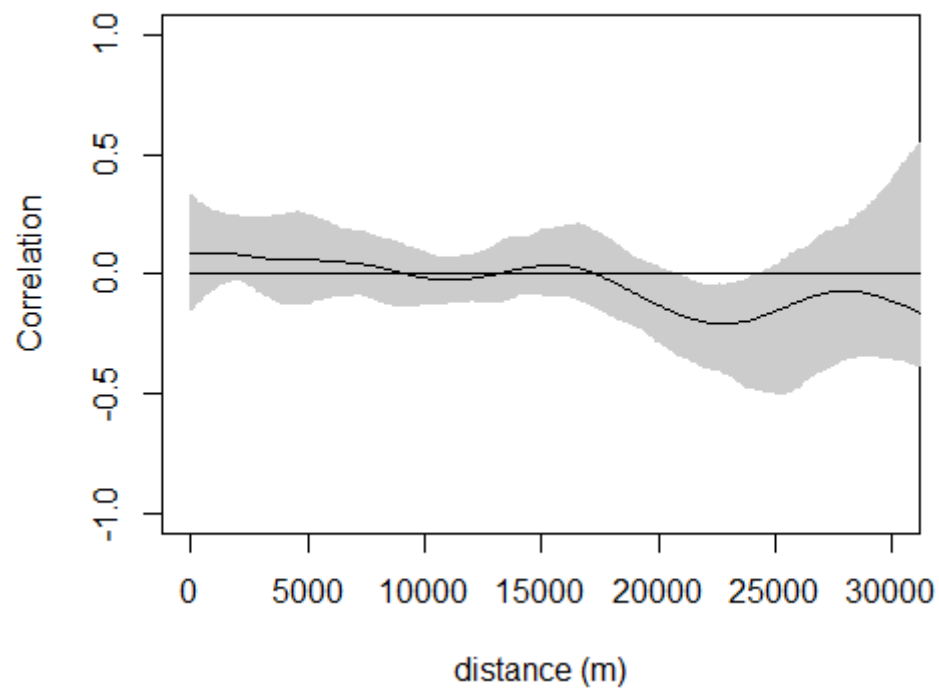
Fjord system	Model formula	Adj R <sup>2</sup>	d.e. (%)
DS	Presence ~ Dist_wall_m	0.00448	0.516
DS	Presence ~ Depth	0.00224	0.348
DS	Presence ~ Slope	0.0005	0.125
DUS	Presence ~ Dist_wall_m	0.027	2.36
DUS	Presence ~ Depth	0.00463	0.487



**Appendix 9.** Logistic regression quantile-quantile plot of simulated model residuals (x-axis) against observed model residuals (y-axis) for the best fitting habitat model using abiotic predictors for bottlenose dolphins in Doubtful Sound. Data was collected during 2018.

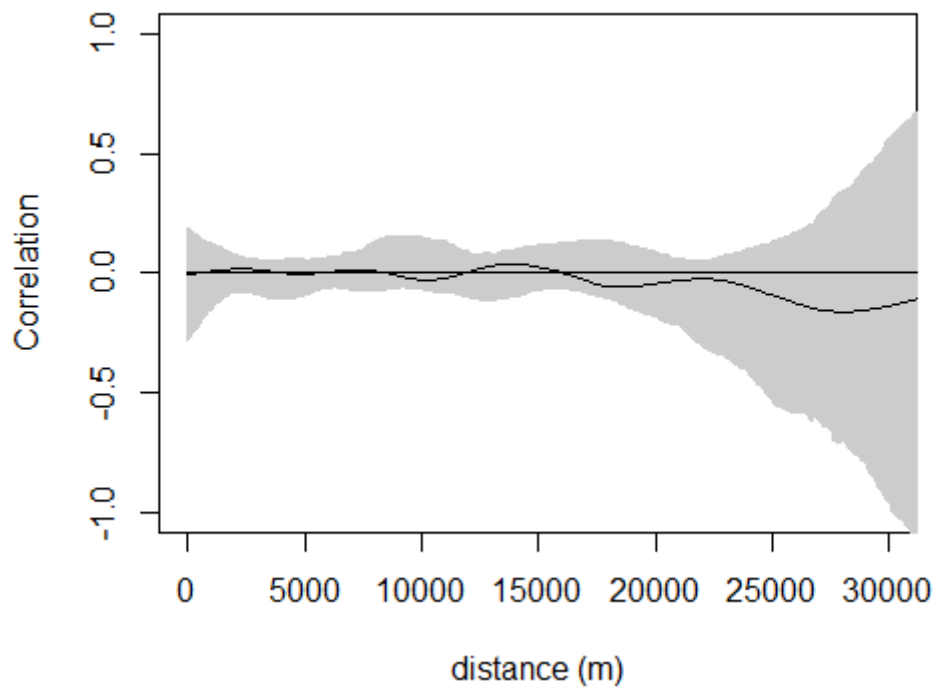


**Appendix 10.** Logistic regression quantile-quantile plot of simulated model residuals (x-axis) against observed model residuals (y-axis) for the best fitting habitat model using abiotic and biotic predictors for bottlenose dolphins in Doubtful Sound. Data was collected during 2018.



**Appendix 11.** Correlogram of residuals for the abiotic-only regression habitat model for bottlenose dolphins in Doubtful Sound for 2018. Shows the correlation between residuals at different distances. The shaded area represents the 95% pointwise bootstrap confidence interval.





**Appendix 12.** Correlogram of residuals for the top biotic and abiotic regression habitat model for bottlenose dolphins in Doubtful Sound during 2018. Shows the correlation between residuals at different distances. The shaded area represents the 95% pointwise bootstrap confidence interval.

**Appendix 13.** Univariate logistic regression model results used in model selection for correlated predictor variables in Doubtful Sound for 2018. Distance from the Entrance (Dist\_Ent\_km), Relative abundance of the five most prevalent fish species (abunT5), diversity measured with Shannon diversity index (Diversity), and the relative abundance of butterfly perch (Butterfly\_perch), scarlet wrasse (Scarlet\_wrasse), girdled wrasse (Girdled\_wrasse) and blue cod (Blue\_cod).

Model formula	Correlated variables	AICc	Adj R <sup>2</sup>	Deviance explained (%)
Presence ~ Dist_Ent_km	Diversity, Butterfly_perch, Girdled_wrasse, Scarlett_wrasse	139.6	0.126	10.7
Presence ~ Diversity	Dist_Ent_km, Girdled_wrasse, Scarlet_wrasse, Blue_cod	118.9	0.086	7.53
Presence ~ abundT5	Butterfly_perch, Girdled_wrasse, Scarlett_wrasse	121.4	0.061	5.45
Presence ~ Butterfly_perch	Dist_Ent_km, abundT5, Scarlett_wrasse	115.2	0.129	11.2
Presence ~ Girdled_wrasse	Dist_Ent_km, Diversity, abundT5, Butterfly_perch, Scarlett_wrasse	104.5	0.196	19.1
Presence ~ Scarlett_wrasse	Dist_Ent_km, Diversity, abundT5, Butterfly_perch, Girdled_wrasse	117.3	0.104	8.74
Presence ~ Blue_cod	Diversity	125.9	0.027	3.73